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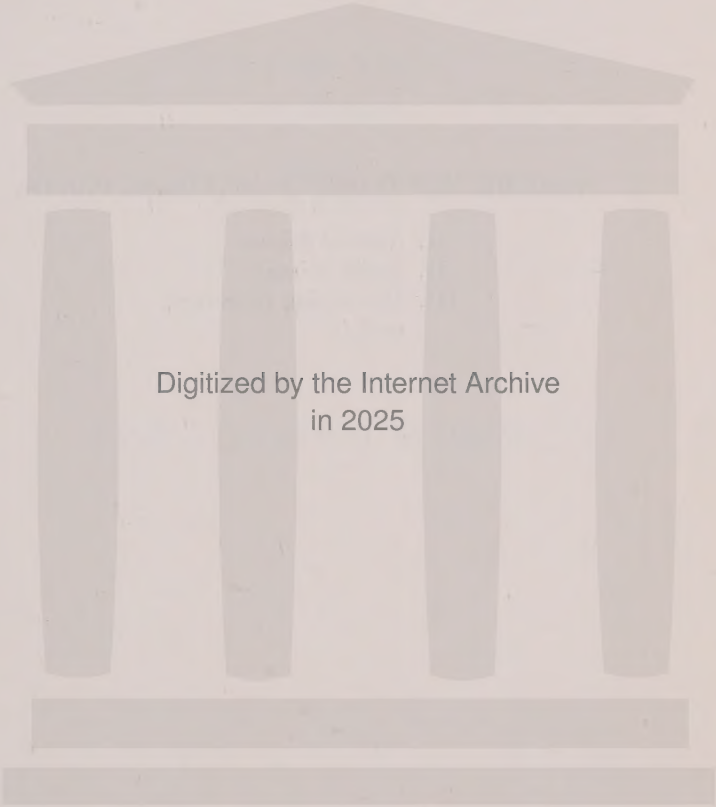
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I. *Natural Science*
II. *Social Science*
III. *Philosophy, Literature, and Art*

Papers of the
MICHIGAN ACADEMY
OF SCIENCE, ARTS, AND LETTERS

VOLUME XLV

(1959 Meeting)

Editor

SHERIDAN BAKER

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PART I

NATURAL SCIENCE

Papers of the Michigan Academy of Science, Arts, and Letters
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MEDICINE

BLOCKING OF VIRAL HEMAGGLUTININS BY SERA FROM CORONARY THROMBOSIS PATIENTS[1]

L. TUNSTALL AND L. H. MATTMAN

Wayne State University

It is established that large numbers of patients who are hospitalized with coronary thrombosis have a history of antecedent or concurrent upper respiratory infections. A significant gap in our knowledge exists in the relationship between these two pathologic conditions. Medical opinion in this regard is fragmentary and contradictory. The basis for divergent views is essentially that it is virtually impossible for the clinician to make an accurate diagnosis of influenza or other viral respiratory infections from the symptomatology alone (Silber, 1958).

A fortunate discovery by Hirst in 1941 has made possible a remarkable progress in the study of the relation of certain animal viruses to animal cells. In harvesting the allantoic fluid of eggs infected with influenza virus, Hirst observed that if blood was shed into virus-containing fluid, the erythrocytes quickly became agglutinated. No such agglutination occurred in uninfected fluids. The agent responsible for this "hemagglutination" is the virus particle itself. The particles are taken up by the red blood cell; this can be shown either by titration of free virus or by observation with the electron microscope of virus adsorbed on the red blood cells. Antivirus serum inhibits this hemagglutination. The inhibitory titer of a serum is related, although not strictly proportional, to its virus-neutralizing titer.

The study of viruses shows that many possess hemagglutinating power. In the present study, however, we employed only those viruses that resemble influenza virus. These agglutinate red blood cells

[1] Publication No. 37 of the Biology Department of Wayne State University. Supported by Michigan Heart Grant No. 32-403-3034 and by an American Medical Association Equipment grant.

directly, the virus particles serving as bridges that hold the cells together.

The following viruses are included:

Influenza Type A strains
- PR 8
- FM 1
- Denver
- Asian

Influenza Type B strains
- Lee
- G. L.

Influenza Type C strain J. J.
Mumps, Enders strain
Newcastle (Parke-Davis)

We used the standard source for virus, that is, the allantoic fluid from egg embryos inoculated two days previously with a small amount of the strains.

Hemagglutination is detected either by an increase in the rate of sedimentation of a suspension of red blood cells measured by the residual turbidity of the supernatant or by Salk's so-called "pattern test" (1944). Nonagglutinated cells sediment into a round solid pellet at the bottom of a test tube, whereas agglutinated cells settle in a characteristic, scattered pattern of sedimentation. A hemagglutination test can be read within an hour or less. The result of a typical method of virus hemagglutination titration and a hemagglutination inhibitor titration is given in Tables I and II.

TABLE I

Method of Virus Antigen Titration*

Dilution of virus	1:32	1:64	1:128	1:256	1:512	1:1024	1:2048	Saline Control
Degree of hemagglutination	4	4	4	4	3	2	0	0

* The titer of the antigen is based on the last tube showing 50 per cent (2+) agglutination.

TABLE II

METHOD OF HEMAGGLUTINATION INHIBITOR TITRATION*

Dilution of serum	1:32	1:64	1:128	1:256	1:512	1:1024	1:2048	1:4096	Saline Control
Degree of hemagglutination	0	0	0	0	0	2	3	4	4

* The titer of the serum is the dilution in which 2+ hemagglutination occurred. The usual inhibitor is antibody.

The development of the immunology of influenza has followed classic lines. First was demonstrated that sera from the patients convalescent from the diseases contained specific antibodies which combine with and neutralize the infectivity of the viral agent. Presuming our coronary sera had antibodies of some type, we tested it against all the stated viruses and found that the inhibition of hemagglutination did occur.

During the course of studies on the inhibition of hemagglutination by immune sera, Francis (1947) observed that when titrations of sera were made, some sera nonspecifically gave blocking unless live virus was used.

Normal serum contains other nonspecific inhibitors of hemagglutination besides the Francis factor. Gottschalk (1951) and Sampaio and Isaacs (1953) have shown that the use of trypsin degrades those mucoprotein inhibitors and avoids the competition between cells and the inhibitor particles for the virus, a reaction which is similar to that of antibody.

In order to obtain specificity in our hemagglutination inhibition, we treated our serum with trypsin and inactivated it at 56 degrees C. for thirty minutes. We also used both inactivated and live virus and were able to demonstrate the ability of coronary sera to prevent viral hemagglutination of the influenza-Newcastle group of viruses. The sera used was from sixty-three coronary cases compared with sera from seventeen patients hospitalized for other conditions. The sera represents cases from three successive years, hence from epidemic and nonepidemic winters for influenza. Some sera were tested after stor-

TABLE III

Coronary Serum Blocking of PR 8 Virus Hemagglutination

Dilution of Serum	1:32	1:64	1:128	1:256	1:512	1:1024	1:2048	1:4096	Saline Control
Hemagglutination:									
with inactivated commercial virus	0	0	0	0	0	0	2	4	4
with inactivated cultured virus	0	0	0	2	3	4	4	4	4
with live virus	0	0	2	2	3	4	4	4	4

age in the frozen state; and some were tested on the days of withdrawal.

Controls did not give an inhibition at a serum dilution of 1:32 or with higher dilutions.

The coronary patients' sera consistently showed some inhibition, and in some cases to a serum dilution of 1:1024. Trypsinizing the serum, which should remove most nonspecific inhibitors, did not, however, prevent virus inhibition. By using the PR 8 strain as the virus source, the presence of inhibitory substance from coronary serum is demonstrated in Table III.

The results of our tests do give weight to the presumption of a relationship between upper respiratory infection and coronary thrombosis. The evidence that post-coronary syndrome might be related to antibody was presented by Dressler in 1956. We must make more studies to determine whether the hemagglutination inhibitor is a normal serum constituent, merely present in an increased amount, or a complement-fixing antibody. The presence of any substance in sera which is constant and definitive may aid in the diagnosis of coronary occlusion.

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Papers of the Michigan Academy of Science, Arts, and Letters
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ZOOLOGY

THE EFFECT OF COLORATION ON GREAT BARRIER REEF ANIMALS[1]

JOSEPH G. ENGEMANN
Michigan State University

Many brilliant-colored fish are normally associated with coral. The explanation of this coloration has been ascribed to concealing coloration by many authors (Dakin, 1950: 108). The main purpose here is to consider the selective advantage of the pattern of a strikingly colored fish, *Chaetodontoplus personifer* (McCulloch) Fraser-Brunner (1933). *C. personifer* is a member of the Chaetodontidae, which Jordan (1908: 613) considers to be one of the most characteristic families of coral reef fishes.

The Role of Natural Selection

Darwin, in his *Origin of Species* (1859: 198), indicates that color can be subject to natural selection. Wallace (1889: 265–266) thought conspicuous colors of tropical fish could either aid concealment among brilliant coral reef organisms or, in some instances, be warning colors. Fisher (1958) has calculated the survival probability for characteristics giving slight selective advantage. Very few introductions of an advantageous trait are needed to assure its continuance. McAtee (1932) concluded that protective adaptations and natural selection were unimportant because predation was in proportion to population and availability. His tables of bird stomach analyses, however, showed that chaetodont fishes were not included in the fish consumed by birds. Poulton (1932) points out the fallacy of assuming no value for protective coloration just because some who have it are consumed.

[1] These observations were made possible by the U. S. Government, which provided a Fulbright Scholarship to Australia, by the Great Barrier Reef Committee, which allowed me to use its facilities on Heron Island, and by Mr. Richard Slack-Smith, who identified the fish and extended many other courtesies. I am indebted to Dr. T. W. Porter for reviewing this paper. Contribution from the Department of Zoology, The University of Michigan.

Since the part sexual selection has played in color and pattern does not readily permit examination, I find it desirable to omit discussion of it by following the same invalid assumption others have used, namely, when male and female have a close correspondence in color and pattern, sexual selection has had little effect. I further assume that brilliant color is not necessarily indicative of a more vigorous physiology and thus selected for on an intraspecific level. The main protective adaptations of coloration in animals are discussed by Cott (1957) as providing concealment, warnings, or mimicry. Mimicry in operation resolves itself into one of the other two categories. I will consider the mode of protection afforded by the color pattern of *C. personifer.*

The Visual Effect of Color

Hue or color is less important in visual apprehension and perception than luminosity contrast (Tinker, 1932). Objects with greater contrast are judged closer than those with less contrast as compared to the background (Mount, et al., 1956). The evidence in both cases is from humans. Proving that fish see exactly what humans do is impossible. But studies like Reighard's (1908) indicate some similarity, probably even color vision. Furthermore, colors may be vivid and contrasting but aid concealment because the pattern blends with the background. Friedmann (1942) discusses such methods of camouflage.

Chaetodontoplus personifer has a blue head with orange spots, a black body, and a yellow caudal fin (Fig. 1). This pattern constitutes warning coloration in coral reef fishes by Bristol's definition (1903). But Thayer (1909) maintains the brilliant colors of reef fishes present an average background picture and thus are concealing colors. Many corals of Heron Island contain algal cells giving them a color similar to the blue head of *C. personifer.* Thus if *C. personifer* were feeding on small invertebrates near the base of such a coral it might look something like Figure 2, with its blue head against the blue algal cells, its black body in the shadow, and its yellow tail superimposed on the bright coral sand. Behavior patterns of other fish suggest that *C. personifer* might take a similar position during periods of danger. The position described would tend to conceal the fish from casual observation.

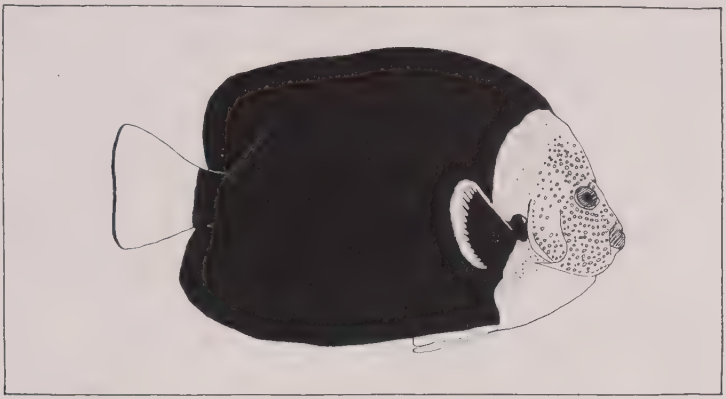

FIG. 1. *Chaetodontoplus personifer*, an angel fish. Length, 19 cm. Coloration: clear area, yellow; black area, black; finely stippled area, pale blue; spotted area, yellowish-orange spots on a blue background.

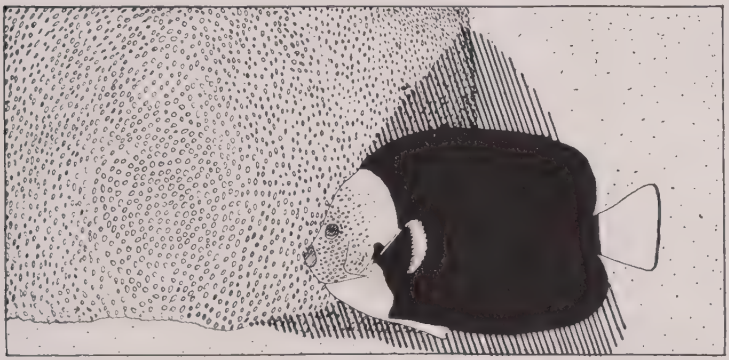

FIG. 2. The hypothetical position of *Chaetodontoplus personifer* in the shadow of a coral colony.

BEHAVIOR

Rabbitfishes (*Siganus* spp.) on Heron Island, when pursued, concealed themselves by taking positions close beside pieces of coral rock. I have observed guppies, pursued by larger aquarium fish, press themselves into the corner of the aquarium. I saw a carp in shallow water in Lake Huron obtain some degree of concealment by

stopping next to an isolated obstruction of smaller width than itself. It remained motionless in that position until actually touched. Apparently, alignment with another object is a frequent position of retreat for fish. In the three cases cited the fish tended to blend with the background or object where they stopped. Breder and Rasquin (1951) observed fish taking positions near background or bottom matching their color. They found the movements of the fish to be rapid and erratic over contrasting bottom. Longley (1918) was able to induce color changes that matched the environment by enticing fish from one environment to another with food. Odiorne (1948) discusses the physiological basis for rapid color change in fish. Color changes in fish are not restricted to providing concealment. Braddock and Braddock (1955) have found a correlation of color with phases of the aggressive behavior pattern in *Betta splendens*. Physiological changes seem unimportant in *C. personifer*, since Rasquin (1958) was not able to produce appreciable change in body color of chaetodont fishes by injecting them with substances capable of altering the pattern of representatives of many other families. Longley (1914) found that bright red fish of the Tortugas reef remained in hiding during the day. From the foregoing examples it is apparent that many fish possess behavior patterns which utilize their coloration. The major predators of fish are other fish. For the effectiveness of warning coloration it is essential for predators to possess a mechanism responsive to warning coloration. Reighard (1908) demonstrated this mechanism in the gray snapper. He could train them to avoid food of a chosen color.

Two kinds of small, dorsoventrally flattened elasmobranchs are commonly found at rest on the bright sandy bottom of the reef around Heron Island. One is a small, flat-headed shark with a light color closely matching the bottom. The other is a ray of much darker color. When the ray settles down on the bottom, however, sufficient sand swirls up from the bottom and settles on the ray to reduce its contrast markedly. Thus its behavior results in partial concealment by sand.

Invertebrate Animals

The invertebrates of many phyla associated with the crinoids of a coral reef resemble the crinoids in color (Potts, 1915). Mollusks are abundant. Most pelecypod shells are similar to the coral sand

in color. *Tridacna*, the giant clam, has a mantle conspicuously colored by algae. The clam closed as quickly when a shadow was passed over it as when it was touched. Closing was less vigorous and less complete when I made vibrations in its vicinity by stomping my feet. The gastropod shells tend to have their brighter colors inside where they are concealed by the body of the animal in life.

The more colorful invertebrates are found on the underside of or among coral rocks. Two major exceptions are the corals and some echinoderms. The corals derive their protection from their stinging cells and sharp skeletons. Conspicuous blue starfish are occasionally found in the open. So is a red species. They are probably protected by their spines as is the more dangerous needle-spined sea urchin.

An interesting puzzle is presented by two types of common large holothuroideans. Frequently several of each are associated with each group of coral colonies. One is a conspicuous black and often is extended on the coral sand. The other is a mottled brown, which blends well with the coral rock, but in the daytime it stays hidden under the rock and at night is as abundant on the coral sand as the black species. Thus it appears that the one possessing concealing coloration does not utilize it during the day.

Discussion and Conclusion

Most authors have considered warning colors distinct from concealing colors. This is not necessarily so, since it is unlikely that distastefulness or other defensive qualities will be repulsive to all predators. Thus a concealing color pattern in a species distasteful to a predator would function as a warning coloration when recognized by the predator. This would probably occur at a closer range than in species lacking effective concealing coloration. I interpret Reighard's (1908) work as indicating that recognition is the essential factor in response to a coloration that experience has revealed to be repellent. Selection for a concealing coloration would be slower in animals having an undesirable attribute capable of recognition as a warning, and not at all when it would increase the chance of their being destroyed or eaten by accident. Obviously, many fish have concealing coloration. I have suggested here that a gaudy color pattern could provide concealment in a restricted situation in the environment of *C. personifer*, and that natural selection in an en-

vironment with constant physical conditions would eventually result in all organisms acquiring coloration to conceal themselves from any enemies with vision they may have. The full extent of concealing coloration among reef animals will not be recognized until we are acquainted with the position, behavior, and environment of each of them.

Summary

The gaudy coloration of *Chaetodontoplus personifer* (McCulloch) is considered in terms of concealing coloration and behavior patterns needed for its effectiveness. Most reef animals have concealing coloration. Natural selection should evolve concealing coloration for most warningly colored forms.

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THE GENUS *ANTICHAETA* HALIDAY, WITH SPECIAL REFERENCE TO THE AMERICAN SPECIES (DIPTERA, SCIOMYZIDAE)

GEORGE C. STEYSKAL
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The genus *Antichaeta* is one of the less common groups of the family Sciomyzidae. It consists of five Palaearctic species and six Nearctic species, including one new species, *Antichaeta fulva*, described below. Only one of the Palaearctic forms has been recorded from this continent, and that record must be considered very doubtful. Only one of the species, *Antichaeta melanosoma*, is fairly common; the others may be considered rare. Of the immature stages, only fragmentary notes on the puparium of *Antichaeta analis* have been recorded, but it is likely that all of the species, like all others in the family that have been observed, are parasitic or predaceous upon fresh-water or land snails.

Antichaeta belongs in the subfamily Tetanocerinae and may be distinguished from other genera by the following characters: propleural bristle not developed; anal cell of wing truncate; vallar bristles lacking; ocellar bristles well developed; hind tibiae with two strong preapical bristles; arista with black hairs; lunule covered; midfrontal stripe broad, shining, complete, sometimes divided down the middle; wing veins *Sc* and R_1 ending well basad of *ta*; only one pair of *dc* bristles present.

The closest related genus is *Hemitelopteryx* Cresson, which is unknown in America, although one of the species of *Antichaeta*, *johnsoni* Cresson, was described in that genus. *Hemitelopteryx* differs from *Antichaeta* in the last two of the above characters, having wing veins *Sc* and R_1 close together, with R_1 ending well basad of *ta*; and having only one pair of *dc*.

Genus *Antichaeta* Haliday

1839, Ann. Nat. Hist., **2**: 187, with one species, *Tetanocera vittata* Hal. (= *Sciomyza analis* Meigen, *teste* Hendel, 1902); Hendel, 1902, Zool.-Bot. Ges. Wien, Abhandl., **2**: 78; Melander, 1920, Entom. Soc. Am., Ann., **13**: 317;

Hendel, 1923, Konowia, 2: 209; Curran, 1934, Fam. Gen. No. Am. Dipt.: 369 (in key, position transposed with *Renocera*); Séguy, 1934, Faune de France, 28: 274; Enderlein, 1939, Deut. Kolon.- u. Uebersee-Mus. Bremen, Veröffentl., 2: 201; Sack, 1939, *in* Lindner, Die Fliegen d. pal. Reg., 5, fasc. 37: 45; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24 (3): 18.

Parantichaeta Enderlein, 1936, *in* Brohmer, Ehrmann, und Ulmer, Die Tierwelt Mitteleuropas, 6: 145, with one species, *Antichaeta bisetosa* Hendel; 1939, Deut. Kolon.- u. Uebersee-Mus. Bremen, Veröffentl., 2: 205. *Subgenus, new status.*

Lioya Enderlein, 1939, Deut. Kolon.- u. Uebersee-Mus. Bremen, Veröffentl., 2: 205. *New synonym.*

KEY TO KNOWN SPECIES OF THE GENUS *ANTICHAETA*

1 (4). Scutellum with 2 bristles; 1 pair of *dc* present
Subgenus *Parantichaeta* Enderlein

2 (3). Thorax yellowish, 2 broad stripes and anterior margin black; fore coxae silvery white (North America)..... *A. johnsoni* (Cresson)

3 (2). Thorax wholly black; fore coxae blackish with silvery sheen (Europe)
A. bisetosa Hendel

4 (1). Scutellum with 4 bristles; 2 pairs of *dc* present..Subgenus *Antichaeta* s.s.

5 (8). Shining interfrontal stripe divided medianly; black species (Europe).

6 (7). One pair of *fo*; parafrontalia dull black; eyes banded in life; legs yellowish red..... *A. atriseta* (Loew)

7 (6). Two pairs of *fo*; parafrontalia reddish yellow; eyes not banded; legs black..... *A. nigra* Karl

8 (5). Shining interfrontal stripe not divided, simple and more or less parallel-sided.

9 (16). Palpi black; upper pleura shining.

10 (11). Antennae with third segment black; reddish yellow species (Europe)
A. analis (Meigen)

11 (10). Antennae with third segment wholly yellowish, no more than upper edge darkened; head, thorax, and abdomen black.

12 (13). With 1 pair of *fo*; front wholly black; *ta* beyond middle of discal cell, at tip of stigma; male postabdomen as in Figs. 1 and 9 (North America)
A. melanosoma Melander

13 (12). With 2 pairs of *fo*, the anterior sometimes much the smaller; front yellowish, at least anteriorly.

14 (15). Front wholly yellow; anterior tarsi blackish, the apical segment yellowish (Europe)..... *A. obliviosa* Enderlein

15 (14). Front blackish, anterior margin more or less yellow; *ta* basad of middle of discal cell and well basad of tip of stigma; tarsi wholly blackish; male epandrium as in Fig. 8 (North America)..... *A. canadensis* (Curran)

16 (9). Palpi yellowish; pleura more or less pruinose above; with 2 pairs of *fo*; largely yellowish species (North America).

17 (18). Antennae with third segment black in apical half; notum not vittate; male postabdomen as in Figs. 2–4..... *A. fulva* Steyskal, sp. nov.

18 (17). Antennae wholly yellowish, third segment at most a little darkened above.

19 (20). Notum wholly yellowish, not vittate; wings uniformly yellowish; male epandrium as in Figs. 5–6. ..... *A. testacea* Melander

20 (19). Notum trivittate with dark gray and yellow; wings almost hyaline, with yellowish anterior border; male epandrium as in Fig. 10.

A. robiginosa Melander

Subgenus *Parantichaeta* Enderlein

Antichaeta bisetosa Hendel

Antichaeta bisetosa Hendel, 1902, Zool.-Bot. Ges. Wien, Abhandl., 2: 78; Sack, 1939, *in* Lindner, Die Fliegen d. pal. Reg., 5, fasc. 37: 46.

Parantichaeta bisetosa (Hendel) Enderlein, 1936, *in* Brohmer, Ehrmann, and Ulmer, Die Tierwelt Mitteleuropas, 6: 145; 1939, Deut. Kolon.- u. Ueberseee-Mus. Bremen, Veröffentl., 2: 205.

Apparently known only from the type locality in the vicinity of Vienna, Austria.

Antichaeta johnsoni (Cresson), comb. nov.

Hemitelopteryx johnsoni Cresson, 1920, Am. Entom. Soc., Trans., 46: 51; Johnson, 1925, Boston Soc. Nat. Hist., Occas. Pap., 7: 250.

I have seen the type from Franconia, New Hampshire, and find that it must be referred here rather than to *Hemitelopteryx*, which genus has not been found in North America. Cresson also noted a female specimen from North Adams, Massachusetts, and Johnson added a record from Briggsville, in the same State. I have also seen two females, one from Hamburg, New York (United States National Museum) and one from Sand Lake, Ontario (Canadian National Collection).

Subgenus *Antichaeta* s.s.

Antichaeta analis (Meigen)

Sciomyza analis Meigen, 1830, Syst. Beschr., 6: 15.

Antichaeta analis (Mg.) Hendel, 1902, Zool.-Bot. Ges. Wien, Abhandl., 2: 79; Séguy, 1934, Faune de France, 28: 274; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24 (3): 18.

Anthichaeta [*sic.*] *analis* (Mg.) Lundbeck, 1923, Dansk. naturh. Fören., Vidensk. Medd., 76: 101.

Tetanocera vittata Haliday, 1833, Ent. Mag., 1: 168; Curtis, 1837, Guide Arrang. Brit. Ins.: 371; Hendel, 1900, Zool.-Bot. Ges. Wien, Verhandl., 1900: 358.

Sciomyza vittata (Hal.) Rondani, 1868, Soc. Ital. Sci. Nat. Milano, Atti, 115: 229; Soc. Nat. Modena, Ann., 47: 10.
Antichaeta vittata (Hal.) Haliday, 1838, Ann. Nat. Hist., 2: 187; Hendel, 1902, Zool.-Bot. Ges. Wien, Abhandl., 2: 79.

This species appears to be rather rare in Europe, known from Sweden, Germany, Galicia, Ireland, England, and Belgium. I have not seen examples. The only American record is one mentioned by Osten-Sacken of a specimen from Massachusetts in the Loew collection, but Aldrich (1905, Cat.: 578) stated that he could not trace the specimen.

Antichaeta atriseta (Loew)

Sciomyza atriseta Loew, 1849, Stettin. Entom. Ztg., 10: 340; Schiner, 1862, Fauna Austr., 2: 48.
Antichaeta atriseta (Loew) Hendel, 1902, Zool.-Bot. Ges. Wien, Abhandl., 2: 80; Séguy, 1934, Faune de France, 28: 274; Sack, *in* Lindner, Die Fliegen d. pal. Reg., 5, fasc. 37: 46.
Lioya atriseta (Loew) Enderlein, 1939, Deut. Kolon.- u. Uebersee-Mus. Bremen, Veröffentl., 2: 209.

Loew did not cite a locality, but it has since been recorded from Germany, Austria, and Livonia. I have not seen examples.

Antichaeta canadensis (Curran), comb. nov.

(Fig. 8)

Pteromicra canadensis Curran, 1923, Canad. Entom., 55: 277; Steyskal, 1954, Mich. Acad. Sci., Arts, Letters, Pap., 39: 269.

Guy E. Shewell first recognized that this species rightfully belongs in *Antichaeta*. I concurred when I saw the types from Banff, Alberta. I have also seen material from Saskatchewan (Saskatoon), Manitoba (Churchill; Wabowden), Ontario (Miners Bay; Moose Factory), Wisconsin (Dane and Washburn Cos.), and Michigan (Sanilac Co., in alder swamp).

Antichaeta fulva Steyskal, new species

(Figs. 2–4)

Male.—Length of wing, 3.5–3.7 mm. Color tawny, only apical half of third segment of antennae, arista, tip of fore tibiae, and preabdomen (segments 1–5), blackish. Bristles and hairs, including

those of arista, black; only squamal ciliae yellow. Wings hyaline, broadly seamed with brownish yellow along veins.

Head: Midfrontal shining stripe simple, a little wider anteriorly; 2 *fo*, anterior pair about half the length of the posterior pair and placed close to them; hairs of arista neither dense nor long.

Thoracic dorsum moderately yellowish-pruinose, with a pair of light brownish median stripes and rather indistinct brownish sublateral areas. Pleura heavily white-pruinose below, thinly so above; wings with *ta* a little beyond middle of discal cell and only slightly before tip of stigma.

Abdomen with terminal part as in Figs. 2–4; 5th sternite with simple, bluntly pointed apical lobe underhanging the postabdomen; epandrium with long, tongue-shaped lobe on dextral side and two short protuberances on sinistral posteroventral margin; dextral surstylus roughly keystone-shaped in lateral view; hypandrium and aedeagus small and simple.

Female.—Length of wing, 3.8 mm. Similar to male; abdomen with segments 1–4 blackish, remainder tawny; fore femora largely pitchy; fore tibiae in apical half and all of fore tarsi black.

Holotype (male) and *allotype*, Ringwood, Dryden, Tompkins County, New York, May 29, 1955 (C. O. Berg and G. Steyskal); male *paratype*, same locality, June 1, 1957 (G. Steyskal), all in my collection.

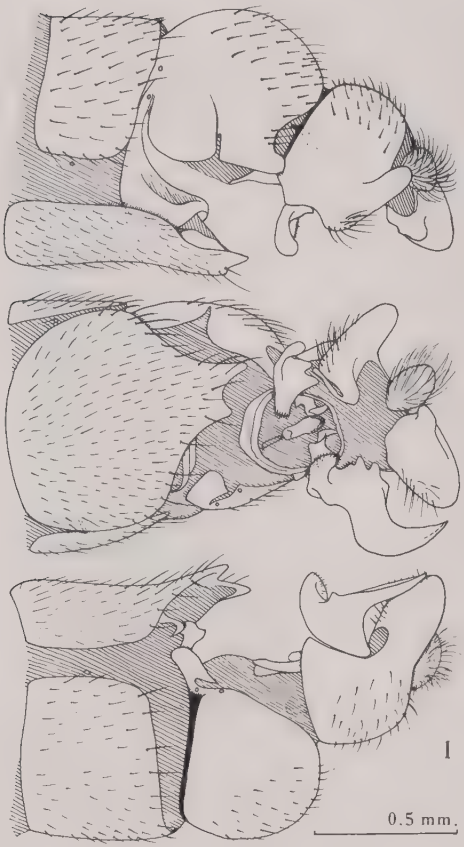
The distinctions cited in the key will suffice to separate this species from its relatives.

Antichaeta melanosoma Melander

(Figs. 1, 9)

Antichaeta melanosoma Melander, 1920, Entom. Soc. Am., Ann., 13: 318; Leonard, 1928, Cornell Univ. Agric. Exper. Sta., Mem., 101: 846; Ouellet, 1941, Nat. Canad., 68: 135.

This seems to be the most abundant species in the genus, ranging from Ontario (Moose Factory; Ottawa; Point Pelee; Simcoe), to Quebec (Aylmer; Berthierville), Wisconsin (Dane Co.; Polk Co., type), Michigan (Clinton, Gratiot, Huron, Iosco, Keweenaw, Kent, Leelanau, Livingston, Midland, Newaygo, Roscommon, Saginaw, Sanilac, Schoolcraft, Tuscola, and Wayne Cos.), Ohio (Delaware), and New York (Beaver Kill; Ithaca).



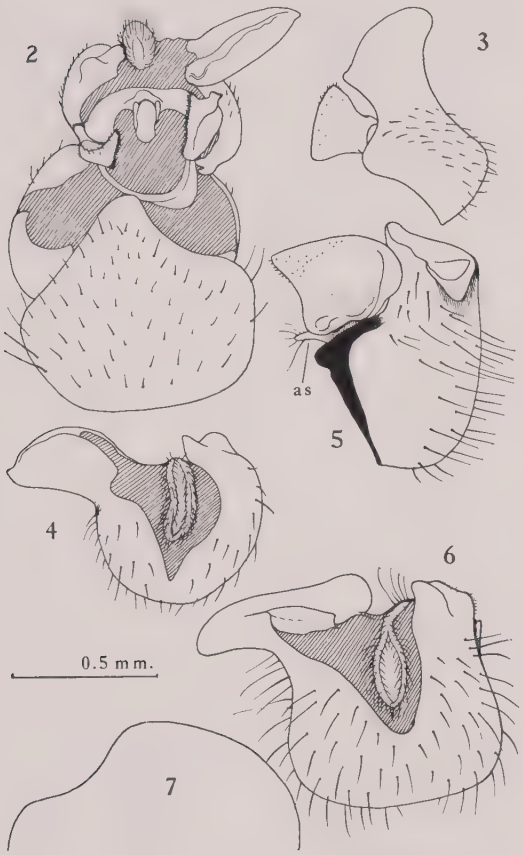
Antichaeta melanosoma Mel., male, Grosse Ile, Michigan

FIG. 1. Apical part of abdomen (fifth segment and postabdomen), sinistral, ventral, and dextral views.

Antichaeta nigra Karl

Antichaeta nigra Karl, 1921, Stettin. Entom. Ztg., 82: 125.
Antichaeta nigroaenea Frey, 1935, Notulae Entom., 15: 97; Sack, 1939, *in* Lindner, Die Fliegen d. pal. Reg., 5, fasc. 37: 85.

A rare European form, described from northeastern Germany, and recorded by Frey from Finland.



Details of Male Abdomen of *Antichaeta* Species

FIGS. 2–4. *Antichaeta fulva*, sp. nov., paratype: 2, ventral view of fifth segment and postabdomen; 3, dextral view of epandrium and surstylus; 4, posterior view of epandrium and proctiger.

FIGS. 5–7. *A. testacea* Mel., Spearfish, South Dakota: 5, dextral view of epandrium and surstyli (*as*—anterior surstylus); 6, posterior view of epandrium and proctiger; 7, outline of posterior half of 5th ventrite.

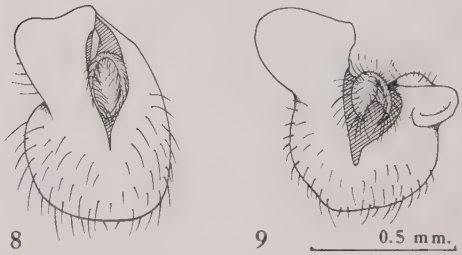


Fig. 8. *Antichaeta canadensis* (Curran), Sanilac County, Michigan: posterior view of epandrium.

Fig. 9. *A. melanosoma* Mel., Grosse Ile, Michigan: posterior view of epandrium.

Antichaeta obliviosa Enderlein

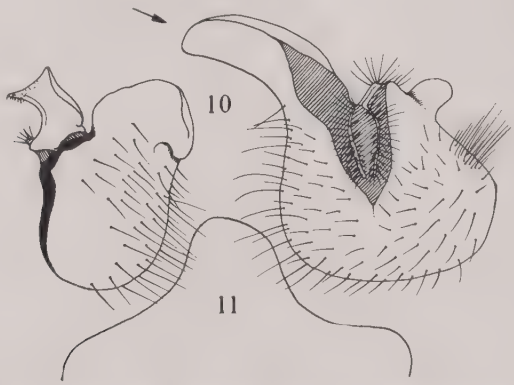
Antichaeta obliviosa Enderlein, 1939, Deut. Kolon.- u. Uebersee-Mus. Bremen, Veröffentl., 2: 209; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24 (3): 18.

Another rare form, described from Berlin, Germany, and cited by Verbeke from Belgium.

Antichaeta robiginosa Melander

(Figs. 10–11)

Antichaeta robiginosa Melander, 1920, Entom. Soc. Am., Ann., 13: 317.



Figs. 10–11. *A. robiginosa* Mel., Roberts, Oregon: 10, posterior view of epandrium with view in direction of arrow, showing surstyli of dextral side; 11, outline of posterior half of 5th ventrite.

This species was described from a female from Three Forks, Montana. I have seen one additional female specimen, somewhat paler than described, from Truro, Nova Scotia, in the Cornell University collections. What is evidently the male of this species is a specimen from Roberts, Marion County, Oregon, March 5, 1940 (R. E. Rieder), from the Oregon State College collections. The figures have been drawn from this specimen.

Antichaeta testacea Melander

(Figs. 5–7)

Antichaeta testacea Melander, 1920, Entom. Soc. Am., Ann., 13: 318.

This species was described from Gallatin County, Montana. I have seen material that agrees well with the description from Spearfish, South Dakota, and Cimarron Canyon, Colfax County, New Mexico.

Phylogeny as Indicated by Postabdominal Structure

The five American species whose postabdomens I have been able to examine exhibit an interesting series of characters which seem to indicate the phylogenetic position of the species. The genus is one of the more highly specialized (apomorphic) of the Sciomyzidae, as shown by the strongly asymmetrical epandrium, the reduced hypandrium and aedeagus, and the extension of the 5th sternite under the postabdomen.

The three yellow forms, *Antichaeta testacea, A. robiginosa*, and *A. fulva* are apparently the least specialized (most plesiomorphic). The asymmetry is least developed, the 5th sternite the least extended, the hypandrium and aedeagus the least reduced. *Antichaeta testacea* and *A. robiginosa* are the only species in which a rudiment of the anterior surstylus (Fig. 5, *as*) is present on the dextral side only. *Antichaeta fulva* is somewhat more specialized than either *A. testacea* or *A. robiginosa*; its hypandrium and aedeagus are more reduced and the anterior surstylus wholly lacking.

Antichaeta canadensis and *A. melanosoma* are closely related and more specialized than either of the preceding three species. Both are extensively black in color, have a well-extended fifth sternite ending in two points, and have a strongly reduced aedeagus and hypandrium. *Antichaeta melanosoma* would appear to be somewhat more

apomorphic than *A. canadensis*, but lack of a prepared postabdomen of the latter forces us to rely on other characters for this conclusion—*A. melanosoma* has developed a wholly black front and has lost the anterior (second) *fo* bristle. However, the development of protuberances of the epandrium in *A. melanosoma* seems to have gone somewhat further than in *A. canadensis*.

The disposition of the spiracles and the development of the sclerites of the 6th and 7th somites in all five species is similar.

When data on the postabdomen of the other species becomes available, an unusually good basis for phylogenetic reconstruction may be presented.

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TAXONOMIC PROBLEMS IN POISON IVY[1]

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In recent years, there has been much study of poison ivy from a non-botanical standpoint. Strauss, Langs, et al. have developed a drug, "Aqua Ivy," as a reasonably certain preventive from the dermatitis (Passenger, Spain, and Strauss, 1956; Gaillard, 1956; Langs and Strauss, 1958; Langs, Strauss, and Fuchs, 1958). Kligman (1958) has written an excellent summary of his own work and that of others on poison ivy dermatitis, its clinicobiology, treatment, and prophylaxis. Epstein and Claiborne (1957) have studied human racial and environmental factors in susceptibility to dermatitis from members of the poison ivy complex. In recent months, the entrance into the United States of Haitian voodoo dolls used as cocktail stirrers has disturbed public health officials, inasmuch as the dolls' heads were made of the toxic cashew nut, a relative of poison ivy, and the eyes of jequirity nuts (Leguminosae), probably more deadly. Charles Dawson has published extensively during the last half decade on the chemistry of the poisons in poison ivy (1954, 1956a, 1956b; Dawson, Wasserman, and Keil, 1946). It has been over two decades since Barkley (1937) published his monograph on the *Rhus* complex and, even yet, his nomenclature is little heeded. The time is thus ripe for a review of poison ivy from a botanical standpoint.

Poison ivy is the northernmost species found in the seven genera of the *Rhus* complex in the Anacardiaceae occurring north of Guatemala—*Actinocheita, Cotinus, Malosma, Metopium, Rhus, Schmaltzia*, and *Toxicodendron* (Barkley, 1937, 1940). It has been recorded as far north as Grand Rapids in Manitoba near Lake Winnipeg (Scoggan, 1957), and as far south as Huehuetenango department in Guatemala (Standley and Steyermark, 1949). It occurs in the Gaspé Peninsula and extends to Vancouver Island (Scoggan, 1950). Outside

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of continental North America, it is found in Bermuda and in the Bahamas. It occurs in every state in the Union, except California, in the taxon accepted as *Toxicodendron radicans*. Several references have been noted to a supposedly native poison ivy in Japan (Greene, 1905; Murakoshi, 1934; Ohwi, 1956). This plant, its taxonomy, and its presence in Japan all need further study. I shall say more about the distribution and habitat preferences of poison ivy when I have delimited the species more clearly.

Barkley (1937) felt that there were sufficiently strong characters consistent within the genus *Toxicodendron* to warrant separating it from *Rhus*. Further, Heimsch (1940, 1942) corroborated this generic distinction on the basis of wood anatomy and pollen morphology. These characters hold for the Asiatic species as well. In addition to the stated characters of nonglandular pubescence of the fruit coat, waxy mesocarp, consistently poisonous resin, and paniculate inflorescence given by Barkley, I have also noted that root hair color is an additional character difference. North American Toxicodendrons have a distinctly brown root with dark brown root hairs. The root hair color of *Rhus*, as opposed to *Toxicodendron*, is generally tawny pink or lighter. The reddish fruit coat of *Rhus* is a fairly consistent character, separating it from the whitish or dun-colored fruit coat of *Toxicodendron* (Barkley, 1957). Poison ivy thus belongs to the genus *Toxicodendron*.

It is interesting to note that previously this plant has been placed by botanists in four genera (not to mention the genus *Edera* [Barkley and Barkley, 1938], where it was first placed by botanists before Linnaeus mistaking it for English ivy, or a close relative). One proposal was a compounded genus, *Rhus-Toxicodendron*, an evident attempt to circumvent the whole problem.

The species epithet is another question entirely. Barkley (1937) lists fifty-three synonyms that have been validly published over the years, including an even baker's dozen published by Greene (1905)! Others, usually referred to by nonbotanists, are often found in dermatological, medical, chemical, or popular journals. One such combination, fortunately attributed to no author, even intimates that poison ivy, poison oak, and poison sumac all form one polytypic species. Whether Barkley's four subspecies are in reality good separations, based on physiological and ecological tests, is a question still to be

answered. In any event, the correct name for poison ivy is *Toxicodendron radicans* (L.) Kuntze (Kuntze, 1891).

The common name poison ivy is usually written as two words, although Harlow (1949) makes a strong case for introducing the one-word spelling. Because of confusion between a poisonous ivy and a name originating from its kinship to English ivy, Harlow suggests the use of "poison-ivy." Fowler (1958) indicates that a hyphen is used to make two words into one: therefore, the more correct form would be a hyphenated word, poison-ivy. Due to common usage and the fact that the literature is saturated with the name spelled as two words, however, it is probably best to regard "poison ivy" as a *nomen conservandum* in a popular sense.

Barkley has also recognized two plants with the common name poison oak (1937). One is *Toxicodendron diversiloba* (Torrey & Gray) Greene, restricted to Washington, Oregon, California, Lower California, and two inland states in Mexico. The second poison oak is *Toxicodendron quercifolia* (Michx.) Greene, found south of an arc from southern New Jersey to Texas. The two poison oaks are allopatric, but they are, except in California, sympatric with *T. radicans*. Hybrids among these forms have been hypothesized by McNair (1925), but no specimens have been cited, nor any artificial hybrids made. The southeastern poison oak and poison ivy have flowering periods that generally do not overlap, whereas the western poison oak and poison ivy have flowering periods which generally do overlap, McNair reports. Since they are all insect-pollinated, there is reason to suspect occasional exchange of genetic material.

Sandy, oak-pine forest is the habitat in which *T. quercifolia* is most likely to occur (Biederman, 1938). On the other hand, poison ivy is not normally abundant in dry, sandy, oak-pine forests although found among pines and other trees in the mountains of Mexico. It is rare in the jack pine forests of Michigan (not listed in the flora by Zimmerman, 1956), and seldom encountered except at bog margins in the New Jersey Pitch Pine Barrens. Martin's studies (1959) at Island Beach, New Jersey, indicate that poison ivy is virtually omnipresent in all habitats but the salt marsh and pine forest type. This suggests that poison oak may be an ecotype of poison ivy, which has, in certain climatic, geographic areas, been able to adapt to the environment of the pine forest type, with accompanying morphological changes.

The western poison oak enjoys a greater variety of soil conditions than any other California shrub, ranging from sandy flats to blue adobe and from gravels to salt marshes. Although it does best on moist hillsides, it, like its eastern counterpart, will tolerate the most sterile soils (Jepson, 1936). Shelmire (1941) grew specimens of the two poison oaks and poison ivy from Wyoming, Nebraska, Texas, and California in his backyard in Texas under "identical conditions of soil, sunshine, . . . and moisture." No constant variation was found in pubescence, tendency to climb, or definite lobation. He concluded from his limited studies that "this variable plant seems best treated taxonomically as a single pleomorphic species with several more or less consistent geographic variations."

Neither of the two recognized poison oak taxa occur in the North Central States, although a "poison oak" is often said to occur there. The name poison oak is frequently applied by laymen to the shrub form and poison ivy to the climbing or herbaceous form, although neither separation is valid in all analyses. Laymen and physicians often diagnose dermatitis venenata from the size of blisters whether poison ivy or poison oak has been the culprit. It is for this reason that many persons believe that poison oak occurs in such states as Illinois and Michigan. "Oak-shaped" leaves have been found on otherwise typical poison ivy in Michigan. Such collections (*Gillis No. 2623*, Ingham Co., Mich., M.S.U. campus, 30 July 1958; *Gillis No. 2846*, Ingham Co., Mich., Baker Woods, M.S.U. campus. Prostrate vine, 26 September 1958) are deposited in the herbarium of Michigan State University. The poison ivy-oak complex is one that demands further investigation to determine the constancy of the variation upon which the species separations are made.

Haack (1940) and Dawson and his co-workers have clearly identified the four poisonous substances in poison ivy as variations in saturation of the alkyl side chain in 3-*n*-pentadecylcatechol (1956a). No work has been done to determine if there is any difference in the chemical nature of the poisons of poison oak, nor, for that matter, of poison sumac (*Toxicodendron vernix*). The Japanese lac tree (*T. vernicifera*) differs in poison chemistry in only one of the four poisons, having two conjugated double bonds in the side chain, a situation not present in the poisons of poison ivy. Inasmuch as I am not susceptible to the poisons of poison ivy and have, indeed, been desensitized by the use of Aqua Ivy as a precautionary measure, yet find myself

"allergic" to poison sumac, there is some evidence that the chemistry of the poisons in poison sumac is different from that of poison ivy.

Hybrids between poison ivy and poison sumac have even been postulated. Such a find would strengthen the concept of their close relation within the same distinct genus. Several plants on the Proud Lake Recreation Area of Oakland County, Michigan, have given evidence of being hybrids between these two species. One plant shows the especially weird combination of three to nine leaflets and a tendency to climb. I am inclined to consider this a juvenile form of poison sumac, but plan further study of transplanted individuals and others in a nearby "hybrid" population.

A five-leaflet poison ivy is known. It has been studied by Barkley (1936) in Texas and grows within the city limits of Houston. Normally the quinquefoliolate leaves are produced as fall approaches. They are pinnately compound, whereas the leaves of the normal, trifoliolate variety are palmately compound. (It is interesting to consider here the difference between a palmately trifoliolate leaf, as in poison ivy, and a pinnately trifoliolate one, as in clover.) A dumping area near Syracuse, New York, is also known to have a quinquefoliolate poison ivy plant (William M. Harlow and John Andresen, personal communication). A five-leaflet poison oak is also described by McNair (1936) as a vigor-response to cutting back in an effort to kill the plant.

Habitat variations probably led to many of the species segregations made over the years. The shrub form is found frequently in open, sunny, dry sites along roads and on sand dunes. The climbing form frequents fencerows and woodlands. There is a "perennial herb" form in which the plant rarely attains a height of 3 to 4 dm. This form predominates farther north, the area around Itasca Park, Minnesota, having only the "perennial herb" form. According to Dr. E. G. Voss in his studies for the publication of the Michigan Flora (personal communication), his specimen *No. 7105*, Manistee Co., Michigan, was collected about as far north as the climbing form occurs in the state of Michigan. The trailing vine form, common in deep shade of mesic woods, is another growth form. The trailing stems may branch extensively and cover several square meters. Occasionally, leaves may be spaced several meters apart on the same trailing stem. Neither the "perennial herb" (subshrub) form nor the trailing vine form flowers regularly.

Geographical variation has some interesting aspects. As one progresses south, he notices little apparent difference in populations of the typical *Toxicodendron radicans*. Plants from southern Michigan may look exactly like those collected in Central Mexico. The fruits in specimens examined from Mexico, however, have a more roughened, brownish appearance than those farther north. In the Southeast, the stems take on a more reddish hue. Vines from Bermuda have distinctly red twigs and petioles, with villous pubescence and a distinct red border on the leaf margins, especially of the young leaves. (Living specimens from Bermuda were sent through the courtesy of I. W. Hughes, Paget East, Bermuda.)

Furthermore, microscopic studies have revealed resin canals in stems, petioles, and even bracts, sepals, and petals (usually three canals in each of the perianth parts). Leaflet size is variable; I have seen variations from 2 to almost 30 cm. for the terminal leaflet. The leaflets tend to be larger on climbing forms, and larger on floodplain sites than elsewhere. The leaves are larger in the sun, contrary to the usual concept of sun and shade leaves. I found an interesting morphological variation at Island Beach State Park, New Jersey, in 1958 (*Gillis No. 2709*, 14 August 1958; *Gillis No. 2791*, 31 August 1958, both from secondary foredune thicket), with feathery structures in the axils of several leaves. A first glance suggested that clusters of opposite, simple leaves comprised the "pinnae" of the feather. Closer examination indicated that these leaves were enlarged primary and secondary bracts, whose flowers failed to develop. In these aborted flowers, the bracts grew to several times their normal length (up to 1.4 cm.) and were arranged like the flowers, occasionally opposite and occasionally alternate.

Vegetatively, poison ivy may occasionally be confused with box elder (*Acer negundo*),[2] virgin's bower (*Clematis virginiana*), fragrant sumac (*Schmaltzia crenata—Rhus aromatica* of Fernald, 1950), strawberry (*Fragaria spp.*), hoptree (*Ptelea trifoliata*), bladdernut (*Staphylea trifolia*), Virginia creeper (*Parthenocissus quinquefolia*), and buckbean (*Menyanthes trifoliata*). The presence of the characteristic fruits and winter buds is the best identifying character in the winter. The angles of leaf venation (lateral veins at 60 degrees from the midvein), absence of attenuate bases on the terminal leaflet, al-

[2] All binomials agree with authors given in Fernald (1950) except those of the Anacardiaceae, which agree with authors given in Barkley (1937, 1940).

ternate leaves, and twig characters are probably the best means of identifying the plant in the growing season. Leaf shape is too variable to be of help.

It can be seen that poison ivy is a problem from the standpoint of nomenclature and clear delimitation of species. The confusions arise in part because of the extreme variation in the species. It is confusing even to the professional botanist, because he may not know it in all its variations and can easily mistake it for other trifoliolate plants. Thus, pity the poor layman, whose error in identification may result in physical torture.

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THE RELATION OF ANTHOCYANINS TO *GAILLARDIA* TAXONOMY[1]

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The rapid development of chromatographic procedures during the past decade has provided a valuable method for separating and identifying organic compounds. This technique has stimulated work on the chemical relationships of species and on the biochemistry of gene action. It is an easily used procedure which may have valuable application in studies of plant and animal evolution. Several papers based on this concept have been published with this end in view.

The interest in chemical differences between species began long before the development of chromatography. Baker and Smith in 1902 and 1920 (Gibbs, 1958) correlated the essential oils of over 100 species of *Eucalyptus* with the morphology of these species and produced an evolutionary sequence based on this relationship. Paper chromatography was not used at this time, but most of the recent work on the subject has been based on this technique. Among the several papers on animal relationships investigated by means of paper chromatography are those of Buzzati-Traverso and Rechnitzer (1953) with fish, Micks (1954) with mosquitoes, and Kirk, Main, and Beyer (1954) with land snails. These workers, analyzing amino-acids and related compounds, found that species differences could be detected in the chromatograms, and that intraspecific races generally gave the same chromatographic patterns. Few papers have appeared on plant chemical relationships, although Roberts and Wood (1958), working with the *Thea* section of *Camellia*, found that two ill-defined species consist of three chemical entities and that the non-*Thea* Camellias are quite distinct from them. The plant investigations of antigen-antibody relationships are more numerous and involve entirely different techniques—not considered here.

The present investigation includes eleven species of *Gaillardia* whose flowers contain anthocyanin. Of these, *G. pulchella* Foug. is

[1] Part of an investigation on the evolution of the genus *Gaillardia*; supported by National Science Foundation Grant G-3943.

one of the best-known species and is widespread in southwestern United States. Its numerous geographic races differ in ray color as well as in morphological characters. This ray color varies from deep red to pink, and differences persist when plants are grown in Michigan. Several other species of the genus produce ray and disk flowers in shades of red and maroon which do not occur in *Gaillardia pulchella*. I suspected that different anthocyanin pigments were the cause of these color variations. Therefore, I have analyzed the colors chromatographically and compared them with the morphological relationships between species.

Methods

Anthocyanins and other compounds were removed from freshly collected rays and disk flowers by boiling in 95 per cent ethyl alcohol which contained 1 per cent HCl. The extract was filtered, evaporated to a dark red liquid, and applied as spots to Whatman No. 1 filter paper strips. The ascending chromatograms were developed in glass cylinders, using a mixture of ethyl acetate:t-butanol:water: glacial acetic acid (5:4:3:1) as the developing solution. All strips were placed in an atmosphere saturated with HCl vapor for two minutes before being run. In most cases two strong anthocyanin bands separated during development in addition to the hydrolyzed cyanidin which traveled near the solvent front. The determination of cyanidin in *Gaillardia* was made by Forsyth and Symmonds (1954). Comparison of the R_f values of several extracts on the same chromatogram indicates which races have anthocyanins in common and which are not identical. Ray and disk extracts of each race must be handled separately, because they contain different pigment mixtures.

Results

All races of *Gaillardia pulchella* tested produced the same chromatographic pattern (Fig. 1) no matter what their geographic origin. Ray extracts separated into two compounds with R_f values of approximately .22 and .28. Disk extracts produced two compounds with R_f values of approximately .22 and .25. It should be noted that these values varied for each chromatogram, and the only accurate way of comparing different extracts was to compare each with a standard, in this case a ray extract of race 1291 from Galveston, Texas. Three anthocyanins were involved in producing the red and orange

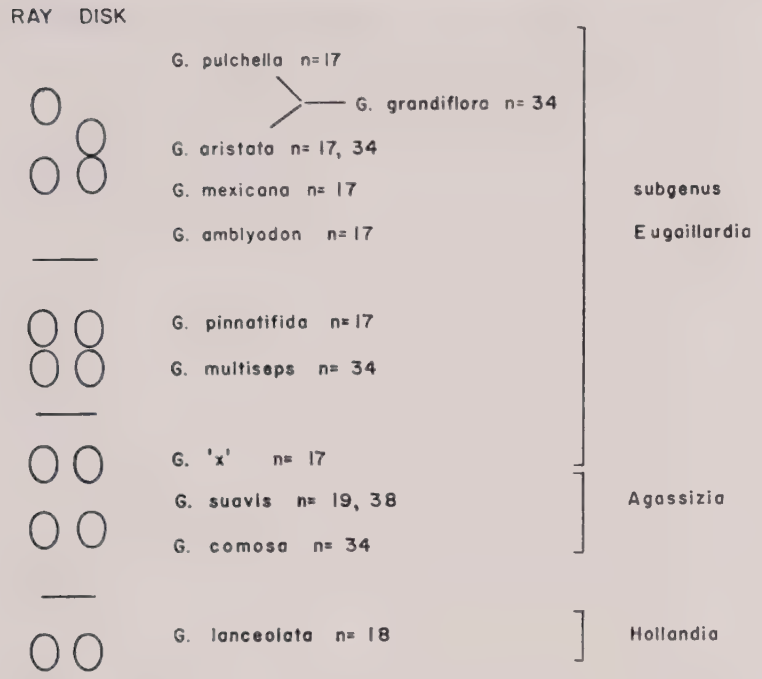

FIG. 1. Relative positions of anthocyanins from ray and disk extracts of eleven *Gaillardia* species.

colors of this species, only one of which was common to both the ray and disk flowers. The color variations in geographic races of *G. pulchella* were apparently due to quantitative differences in these three pigments.

Four other species—*Gaillardia aristata* Pursh., *G. grandiflora* Van Houtte, *G. mexicana* Gray, and *G. amblyodon* Gay—produced pigments at locations identical with those of *G. pulchella* when their extracts were run on the same chromatogram. These species are closely related morphologically, and *G. pulchella* has been experimentally hybridized with each, indicating fairly close relationship.

Races of *Gaillardia pinnatifida* Torr. and *G. multiceps* Greene have similar compounds in both ray and disk flowers, and these correspond to the pigments in *G. pulchella* disk flowers. All species con-

sidered so far belong to the morphological subgenus *Eugaillardia* (Biddulph, 1944).

Ray and disk flowers of *Gaillardia suavis* (Gray and Engelm.) Britt. and Rusby, *G. comosa* Gray, and an undescribed species "X" contain the same pigments, and these correspond to the ray pigments of *G. pulchella*. The first two species are included in the subgenus *Agassizia*. The undescribed species belongs on morphological grounds to subgenus *Eugaillardia* but its anthocyanins correspond to those of *G. suavis* and *G. comosa*.

The third subgenus, *Hollandia*, includes the species *Gaillardia lanceolata* Michx., whose ray and disk flowers contain only one anthocyanin with a R_f of .22, and this corresponds to one of the pigments in the other subgenera.

In order to determine whether these species contained the cyanin molecule, the separate bands were clipped out of the chromatogram, eluted with ethyl alcohol, evaporated to dryness, and hydrolyzed five minutes at 100 degrees C. in 50 per cent HCl. These preparations were evaporated, applied to a chromatogram, and run in the previously described solvent. Cyanidin appeared in all cases, and the species differences are therefore due to different sugars or related substances in the side chains of the molecule.

Conclusions

Gaillardia species with red rays can be separated into four groups on the basis of the anthocyanin mixtures present in ray and disk flowers, and these groups contain species closely related on the basis of their morphology. The only departure from this close correlation is the undescribed species which is morphologically closest to the *G. pinnatifida–G. multiceps* group of subgenus *Eugaillardia*, but whose anthocyanin complex is like that of the *Agassizia* subgenus. The chemical differences in ray color closely parallel the morphological differences and provide another tool for analyzing species relationships. A study of other classes of organic compounds would probably yield considerably more information on species relationships.

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POLLEN SPECTRA FROM BRYOPHYTIC POLSTERS, INVERNESS MUD LAKE BOG, CHEBOYGAN COUNTY, MICHIGAN[1]

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Ever since the application of pollen analysis to the study of postglacial vegetation history we have been concerned about improvement of our interpretations of fossil pollen records. We are well aware of the wide variation in production of pollen and spores by different species and of the vagaries of transport of these minute bodies by wind and water (Cain, 1939). But the proven usefulness of the pollen analytical method in paleoecology, especially in the postglacial sediments of northwestern Europe and eastern North America, demonstrates that pollen spectra do reflect significant features of the vegetation of local areas when carefully interpreted. One approach to improving our interpretation of spectra of fossil pollen is through correlation of modern pollen rain with existing vegetation that contributes the pollen and spores.

A common method for sampling the modern pollen rain for specific sites is analysis of pollen and spores lodged in bryophytic polsters (Carroll, 1943; Potzger, Sylvio, and Hueber, 1956). Moss polsters, at least in constantly moist habitats, provide surfaces on which pollen lodges and is more or less protected against decay. Polsters on bog surfaces presumably hold the pollen that will eventually be incorporated in accumulated peat as microfossils. The term of life of moss polsters undoubtedly varies with the moss species and the habitat, but polsters of living stems of *Sphagnum* in bogs probably contain pollen from no more than the past ten years.

In this study I used bryophytic polsters to analyze the modern pollen rain at seven stations in Inverness Mud Lake Bog, Cheboygan County (Secs. 7 and 18, Inverness Tp., T. 37 N., R 2 W.), in the north-

[1] The field surveys and collections were made while the author was on the faculty of the University of Michigan Biological Station, and the laboratory work was performed in part through research assistance supported by the Horace H. Rackham Fund of the University of Michigan.

ern part of the Lower Peninsula of Michigan. Detailed phytosociological lists of the vegetation in the vicinities of the bryophytic polster localities permit detailed comparison of the spectra with the very local flora; and pollen profiles from the peat deposit in Inverness Mud Lake Bog (Sears, 1942) and from the bottom sediments in Douglas Lake (Wilson and Potzger, 1943) in southwestern Cheboygan County permit comparisons with the youngest fossil spectra that have been described for this region.

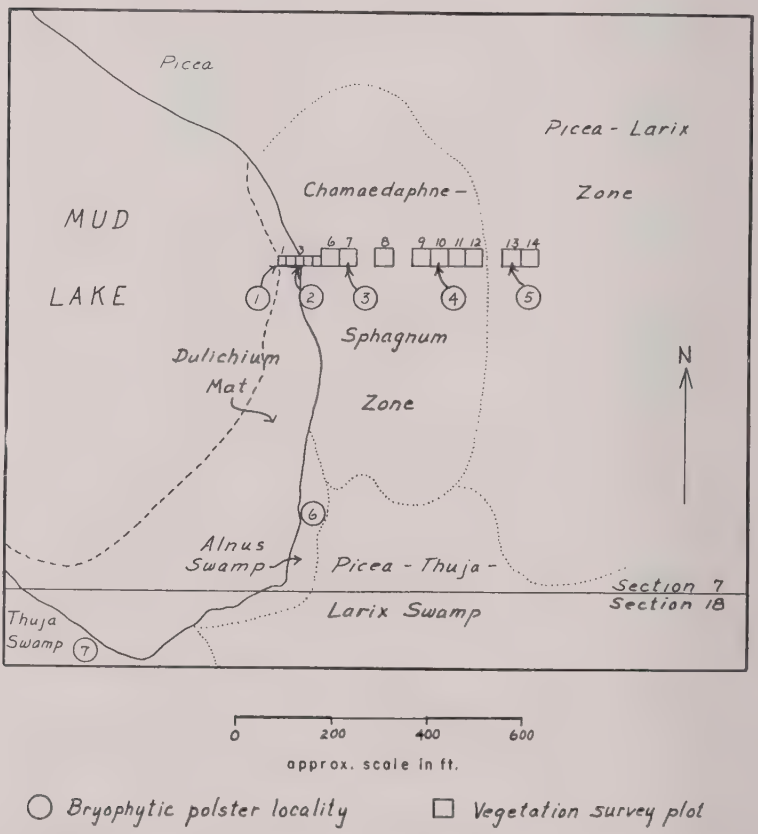

FIG. 1. Sketch map of Inverness Mud Lake Bog, showing localities at which bryophytic polsters were collected and plots for which vegetation surveys were made.

Methods

The sketch map of Inverness Mud Lake Bog, Figure 1, shows the locations from which bryophytic polsters were collected after a survey of fourteen vegetation plots by the students in my ecology class from the University of Michigan Biological Station on 13 July 1957. The phytosociological lists from these plots are presented in Tables I through V. I am indebted to Frederick B. Bevis for phytosociological lists which he made in 1958 in the vicinity of bryophytic polster stations 6 (*Alnus* Swamp, Table VI) and 7 (*Thuja* Swamp, Table VII) (Bevis, 1959). Mr. Bevis also furnished identifications of some of the lichens and mosses listed in Tables I through V.

TABLE I

Phytosociological Lists from Vegetation Survey Plots 1 and 2, *Dulichium* Mat Zone*

Polster No. 1, 13 July 1957

Survey by	Anderson	Gebben
Plot No.	1	2
Plot size (m)	3 × 5	7 × 5
Herb stratum		
Dulichium arundinaceum	3.5	3.4
Eleocharis olivacea	1.5	—
Nymphaea odorata	3.4	—
Lysimachia terrestris	+.1	—
Carex lasiocarpa	1.3	3.4
Hypericum virginicum	+.1	2.3
Lycopus virginicus	1.3	2.4
Eleocharis acuminata	1.2	+.2
Carex comosa	+.2	+.2
Sium suave	—	+.1
Potentilla palustris	—	+.2
Campanula aparinoides	—	+.1
Galium trifidum	—	+.1
Epilobium strictum	—	+.1
Viola cf. pallens	—	+.3
Ground stratum		
Calliergon stramineum	+.3	2.3

* Addition of -- beneath the sociability value 3, 4, or 5 indicates that the patch, colony, or stand is interrupted or penetrated by other species locally.

TABLE II

PHYTOSOCIOLOGICAL LISTS FROM VEGETATION SURVEY PLOTS 3, 4, AND 5, *CHAMAEDAPHNE* ZONE ADJACENT TO *DULICHIUM* MAT*
Polster No. 2, 13 July 1957

Survey by	Heatwole	LaRoi	Farmer
Plot No.	3	4	5
Plot size (m)	3 × 5	5 × 5	5 × 5
Tree stratum			
Picea mariana	—	2.1	3.1
Larix laricina	—	2.2	1.1
Shrub stratum			
Chamaedaphne calyculata	4.5	4.4	3.3
Andromeda glaucophylla	+.3	+.2	2.2
Alnus rugosa	+.2	—	—
Amelanchier sp.	—	+.1	—
Vaccinium myrtilloides	—	r.1	—
Kalmia polifolia	—	+.2	2.3
Herb stratum			
Acer rubrum (seedling)	—	r.1	—
Thuja occidentalis (seedling)	—	r.1	—
Lythrum salicaria	+.1	—	—
Carex lasiocarpa	2.4	—	—
Lysimachia terrestris	+.1	—	—
Lycopus virginicus	+.1	—	—
Carex comosa	+.2	—	—
Sium suave	+.2	—	—
Campanula aparinoides	+.1	—	—
Epilobium strictum	+.1	—	—
Viola cf. pallens	+.2	—	—
Scirpus cf. cyperinus	+.2	—	—
Poa sp.	+.2	—	—
Calla palustris	+.4	r.1	—
Carex disperma	—	1.2	—
Carex trisperma	—	+.2	—
Calamogrostis sp.	—	r.2	—
Lycopus uniflorus	—	r.1	—
Rhynchospora alba	—	1.3	2.4
Eriophorum virginicum	—	+.2	1.2
Calopogon pulchellus	—	+.1	+.1
Sarracenia purpurea	—	r.1	2.2
Cypripedium acaule	—	+.1	+.1
Habenaria blephariglottis	—	—	+.1
Carex pauciflora	—	—	+.2
Menyanthes trifoliata	—	—	2.2
Ground stratum			
Vaccinium oxycoccus	—	1.2	1.3
Sphagnum magellanicum, S. warnstorfianum, S. spp.	—	4.4	5.5
Undet. mosses	—	+.3	—
Cladonia sp.	—	+.2	—

* *Ibid.*

TABLE III

PHYTOSOCIOLOGICAL LISTS FROM VEGETATION SURVEY PLOTS 6, 7, AND 8, *CHAMAEDAPHNE–SPHAGNUM* ZONE*

Polster No. 3, 13 July 1957

Survey by	Marks	Quaynor	Seda del Toro
Plot No.	6	7	8
Plot size (m)	10 × 10	10 × 10	10 × 10
Tree stratum			
Picea mariana	2.4	—	3.3
Larix laricina	+.2	—	2.3
Shrub stratum			
Chamaedaphne calyculata	3.5	4.3	3.4
Andromeda glaucophylla	2.3	3.3	2.3
Gaylussacia baccata	—	1.2	—
Vaccinium myrtilloides	—	+.2	—
Kalmia polifolia	—	—	2.3
Herb stratum			
Picea mariana (young)	—	2.1	—
Larix laricina	—	2.1	—
Eriophorum virginicum	1.1	1.2	1.2
Sarracenia purpurea	1.2	2.1	1.2
Habenaria blephariglottis	1.1	+.1	1.1
Cypripedium sp.	1.2	+.1	—
Pogonia ophioglossoides	1.2	—	—
Calopogon pulchellus	+.1	1.1	—
Scheuchzeria palustris	+.1	—	—
Carex pauciflora	+.3	—	—
Menyanthes trifoliata	1.3	—	—
Rhynchospora alba	2.3	—	2.3
Eriophorum spissum	—	—	+.2
Ground stratum			
Gaultheria hispidula	—	1.2	—
Vaccinium macrocarpon	2.4	1.2	2.3
Vaccinium oxycoccus	1.3	1.4	—
Drosera rotundifolia	1.3	—	1.3
Sphagnum magellanicum, S. warnstorfianum, S. spp.	4.4	4.5	4.5
Epiphytes			
Parmelia physodes	+.1	r.1	+
Cetraria pinastre	+.3	—	+
Evernia sp.	+.2	+	—
Alectoria sp.	+.3	—	—

* *Ibid.*

TABLE IV

PHYTOSOCIOLOGICAL LISTS FROM VEGETATION SURVEY PLOTS 9, 10, AND 11, *CHAMAEDAPHNE–SPHAGNUM* ZONE*

Polster No. 4, 13 July 1957

Survey by	Mensah	Wunderlich	Franklin
Plot No.	9	10	11
Plot size (m)	10 × 10	10 × 10	10 × 10
Tree stratum			
Picea mariana	—	—	3.3
Larix laricina	—	—	1.1
Shrub stratum			
Chamaedaphne calyculata	3.4	4.4	4.4
Andromeda glaucophylla	1.3	1.2	2.3
Kalmia polifolia	2.4	—	1.3
Ledum groenlandicum	+.2	r.2	+.2
Herb stratum			
Picea mariana (young)	2.1	1.3	—
Larix laricina (young)	—	1.1	—
Rhynchospora alba	2.3	+.2	2.2
Sarracenia purpurea	2.3	+.3	2.2
Habenaria blephariglottis	1.1	+.1	1.1
Scheuchzeria palustris	+.2	+.1	—
Carex pauciflora	—	+.2	—
Eriophorum spissum	—	+.3	+.3
Cypripedium sp.	—	—	+.1
Ground stratum			
Gaultheria hispidula	r.2	+.3	—
Vaccinium macrocarpon	2.3	+.2	—
Vaccinium oxycoccus	—	—	2.2
Drosera rotundifolia	1.2	+.3	+.3
Sphagnum magellanicum, S. warnstorfianum, S. spp.	4.4	5.5	5.5
Epiphytes			
Evernia mesomorpha	—	—	+
Cetraria pinastre	—	—	+
Cetraria sepincola	—	—	+
Alectoria nidulifera	—	—	+
Alectoria jubata	—	—	+
Parmelia physodes	—	—	+

* *Ibid.*

TABLE V

PHYTOSOCIOLOGICAL LISTS FROM VEGETATION SURVEY PLOTS 12, 13, AND 14, *PICEA–LARIX* ZONE*

Polster No. 5, 13 July 1957

Survey by	Hodson	Kepner	Bell
Plot No.	12	13	14
Plot size (m)	10 × 10	10 × 10	10 × 10
Tree stratum			
Picea mariana	3.2	3.2	3.2
Larix laricina	2.1	1.1	—
Shrub stratum			
Chamaedaphne calyculata	3.2	2.2	4.4
Ledum groenlandicum	2.3	3.2	1.1
Kalmia polifolia	1.1	1.1	1.1
Vaccinium myrtilloides	1.1	1.1	+.1
Andromeda glaucophylla	1.1	1.1	—
Herb stratum			
Eriophorum spissum	1.2	+.2	+.1
Eriophorum virginicum	1.1	—	—
Sarracenia purpurea	+.1	+.1	+.1
Calopogon pulchellus	r.1	r.1	r.1
Habenaria blephariglottis	—	r.1	+.1
Carex trisperma	—	r.2	+.1
Scirpus sp.	—	+.1	—
Cypripedium acaule	—	—	+.1
Ground stratum			
Gaultheria hispidula	1.3	1.1	+.1
Vaccinium macrocarpon	—	1.1	+.1
Drosera rotundifolia	—	r.1	+.2
Sphagnum magellanicum, S. warnstorfianum, and undetermined spp.	4.4	5.5	4.4
Calliergonella schreberi	2.4	—	2.3
Dicranum bergerii	+.3	—	+.3
Cladonia spp.	1.3	+.2	+.3
Epiphytes			
Arceuthobium pusillum	—	—	+
Evernia mesomorpha	+	+	+
Cetraria pinastre	+	+	+
Cetraria sepincola	+	+	+
Alectoria nidulifera	+	+	+
Alectoria jubata	+	+	+
Parmelia physodes	+	+	+

* *Ibid.*

TABLE VI

PHYTOSOCIOLOGICAL LIST FROM *ALNUS* SWAMP
(FROM BEVIS, 1959)
Polster No. 6, July 1958

Survey by	Bevis
Plot size (m)	2 × 2
Shrub stratum	
Alnus rugosa	4.3
Nemopanthus mucronata	1.2
Salix spp.	+.4

The vegetation surveys were made by means of phytosociological lists (*relevés*) according to the Braun-Blanquet method of notation (Braun-Blanquet, 1932; Ellenberg, 1956). This method requires listing of all observable plant species, and evaluation of cover abundance (first symbol or number in the notation) and "sociability" or gregariousness (second number in the notation). The scale of values for cover abundance is as follows:

*Value**	*Condition of abundance or cover for the species*
5	Covering more than 75 per cent of the sampled area
4	Covering 50 to 75 per cent of the sampled area
3	Covering 25 to 50 per cent of the sampled area
2	With any number of individuals covering 5 to 25 per cent of the sampled area, or very numerous individuals but covering less than 5 per cent of the area
1	Numerous, but covering less than 5 per cent of the sampled area, or fairly sparse but with greater cover value
+	Sparse and covering only a little of the sampled area
r	Very rare and covering only a very little of the sampled area (usually only one example)

The scale of values for sociability, which indicates the pattern of distribution of the individuals, is as follows:

*Value**	*Condition of "sociability" (gregariousness) for the species*
5	In large solid stands; very dense populations
4	In small colonies or larger mats; rather dense populations
3	In small patches or polsters; distinct groups
2	In small groups or clusters
1	Growing singly

* Addition of -- beneath the sociability value 3, 4, or 5 indicates that the patch, colony, or stand is interrupted or penetrated by other species locally.

TABLE VII

PHYTOSOCIOLOGICAL LIST FROM *THUJA* SWAMP
(FROM BEVIS, 1959)
July 1958

Survey by	Bevis
Plot size (m^2)	120
Tree stratum	
Thuja occidentalis	4.1
Abies balsamea	1.1
Acer rubrum	1.1
Betula lutea	r.1
Picea mariana	r.1
Shrub stratum	
Taxus canadensis	2.3
Acer spicatum	1.1
Amelanchier sp.	r.1
Herb stratum	
Coptis groenlandica	2.3
Rubus pubescens	1.2
Aralia nudicaulis	1.1
Galium aparine	1.2
Maianthemum canadense	1.1
Linnaea borealis	+.1
Trientalis borealis	+.1
Clintonia borealis	+.1
Athyrium filix-femina	+.3
Goodyera repens	r.1
Pyrola rotundifolia	r.1
Mitchella repens	r.1
Habenaria hyperborea	r.1
Dryopteris spinulosa	r.1
Erythronium americanum	r.1
Dryopteris marginalis	r.1
Ground stratum	
Mnium punctatum var. elatum	1.5
Mnium punctatum	+.4
Thuidium recognitum	+.5
Sphagnum magellanicum	+.5
Sphagnum wulfianum	+.5
Bazzania trilobata	+.5
Radula complanata	+.4
Heterophyllum haldnianum	r.1
Cladonia cristatella	r.1
Epiphytes	
Parmelia sulcata	r.1
Parmelia rudecta	r.1
Parmelia physodes	r.1
Bacidia muscorum	r.1
Usnea florida	r.1
Cetraria sepincola	r.1

The bryophytic polsters collected were all of *Sphagnum* except No. 1, which was a polster, or rather a mass of the living mat, of *Calliergon stramineum*. Only the uppermost and living portions of each polster were taken in order to avoid contamination from fossil pollen in underlying peat. The polsters were immediately sealed in individual waxed-paper bags, in which they were dried without heat for a period of five days before storing. The collecting bags were later opened in the laboratory, and the polsters were individually stirred up in large beakers with a solution of trisodium phosphate (0.5 per cent by weight) in distilled water (Benninghoff, 1947) to free the pollen and spores from the larger moss fragments. The sediment dislodged from each polster was then centrifuged, boiled three minutes in 5 per cent KOH solution, washed with glacial acetic acid, subjected to the Erdtman acetolysis procedure (Erdtman, 1943), washed with distilled water, and mounted in glycerin jelly on microscope slides.

Pollen counts were made by traverses back and forth across the slide preparations at precise settings of the calibrated mechanical stage under a 40× objective with 10× oculars. A reference point was marked with India ink in the lower left-hand corner of the cover glass of each preparation, and its position was recorded in terms of the mechanical stage calibration. In this way, the mechanical stage coordinates for any grain of interest could be used for relocating that grain on any microscope employing the millimeter scale on its mechanical stage. Counting of a preparation was continued until at least 100 grains of tree pollen were counted. With nonarboreal pollen and spores and undetermined grains the total count was 250 to 300 for most preparations. After more than 100 tree grains had been counted, two slide preparations were thoroughly searched for additional types of pollen and spores; new types found in this search were assigned "trace" (tr) values. Pollen analysts differ in their practices in regard to the minimum numbers of grains counted, depending in part upon the nature and geographic origin of the material. With bryophytic polster material I have found that the above-described practice results in a reliable sample, as further counts have failed to increase the "trace" categories to more than 1 per cent or to significantly alter the values for grains present in larger proportions.

Percentage values for the categories of pollen and spores were calculated on the basis of total tree pollen (ΣAP) as 100 per cent. Fungus spores, although counted under the microscope, are not presented

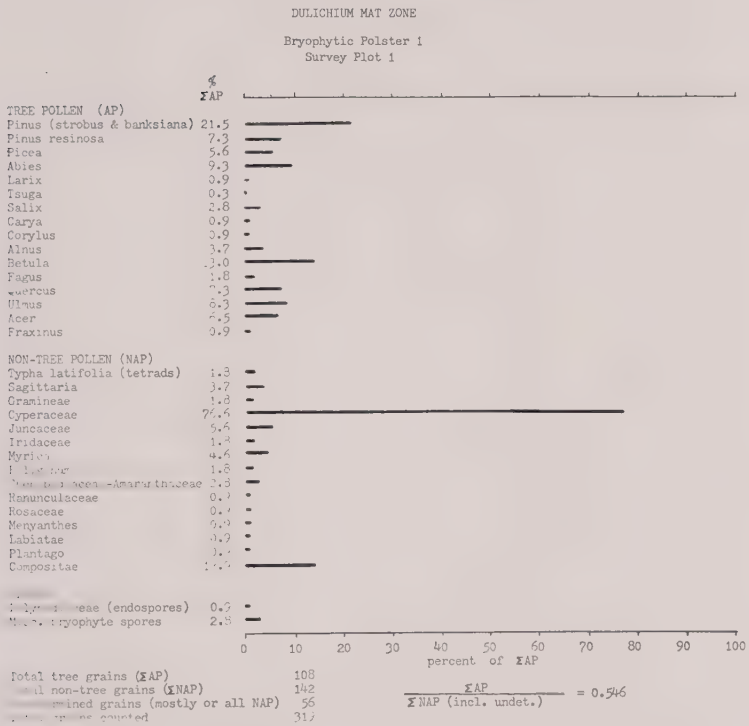

FIG. 2. Pollen spectrum of Bryophytic Polster No. 1 collected on Vegetation Survey Plot 1 in the *Dulichium* Mat Zone.

in the tabulated results (Figs. 2 through 8), as their identities could not be determined and their significance was therefore left in doubt. The pollen and spore categories shown in Figures 2 through 8 are at the limit of determination possible with the reference slide collections and literature available to me. Thus, "Sparganium-Typha" represents single grains like those of *Typha angustifolia* and of several species of *Sparganium*, but I could not find characters by which to further resolve the determination. The "Carya" could be any one of several species in the genus, but the *Juglans cinerea* grain is distinct from *J. nigra* and could be resolved to the species. *Corylus* and *Alnus*, usually placed in the nonarboreal pollen (NAP) category in

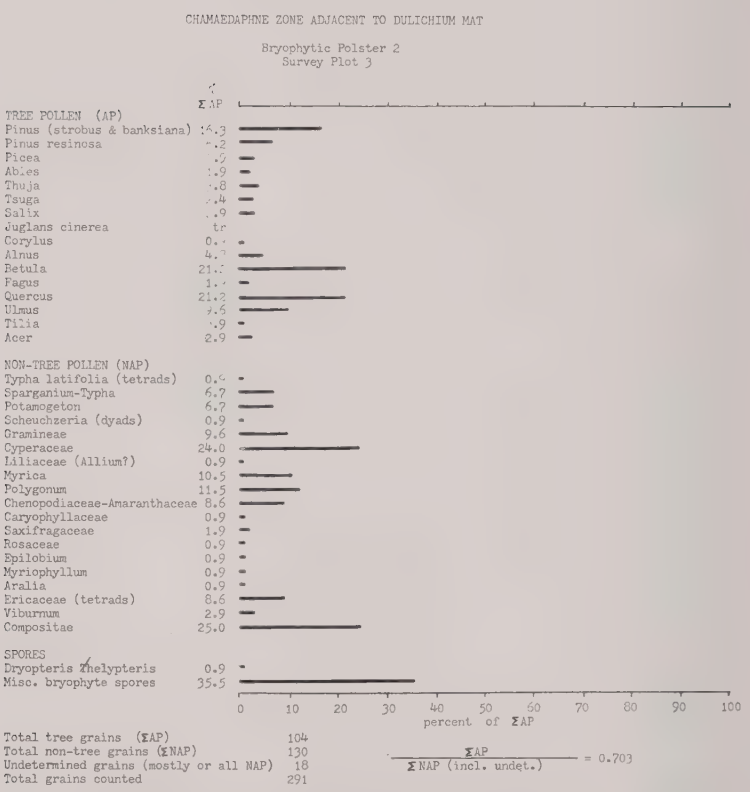

FIG. 3. Pollen spectrum of Bryophytic Polster No. 2 collected on Vegetation Survey Plot 3 in the *Chamaedaphne* Zone adjacent to the *Dulichium* Mat.

forested region studies, were included with the arboreal pollen (AP) because their pollen is commonly distributed as widely as that of the heavily producing forest trees, in contrast to the short-range distribution of most nonarboreal pollen (Gramineae and Compositae excepted). *Pinus resinosa* pollen was distinguished from the other pine species of the region (*P. strobus* and *P. banksiana*) by the presence of a thickened, scalloped fringe around the margin of the cap on the body of the bisaccate grain. With fossil pollen, of course, one could not so safely assume that only certain species have contributed the pollen,

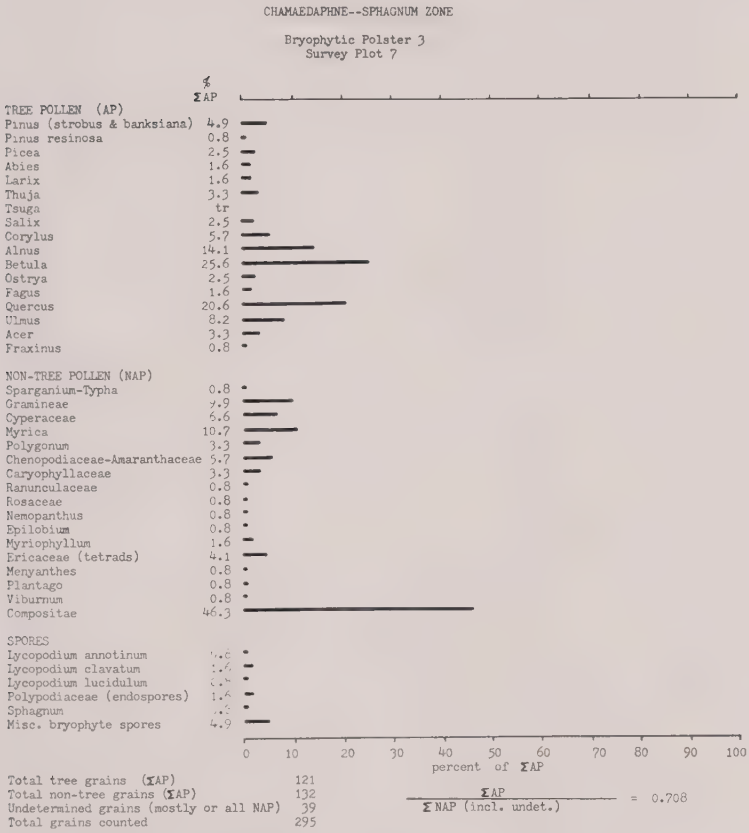

FIG. 4. Pollen spectrum of Bryophytic Polster No. 3 collected on Vegetation Survey Plot 7 in the *Chamaedaphne-Sphagnum* Zone.

and this treatment might not be recommended. The ratio of AP: NAP was calculated for each preparation and is presented with the spectra in Figures 2 through 8. This ratio is often useful in pollen statistics for evaluation of the relative prevalence of forest over non-forest vegetation. In these samples this ratio varied from 0.457 to 0.894, a reflection of the relative contribution of local AP or NAP component.

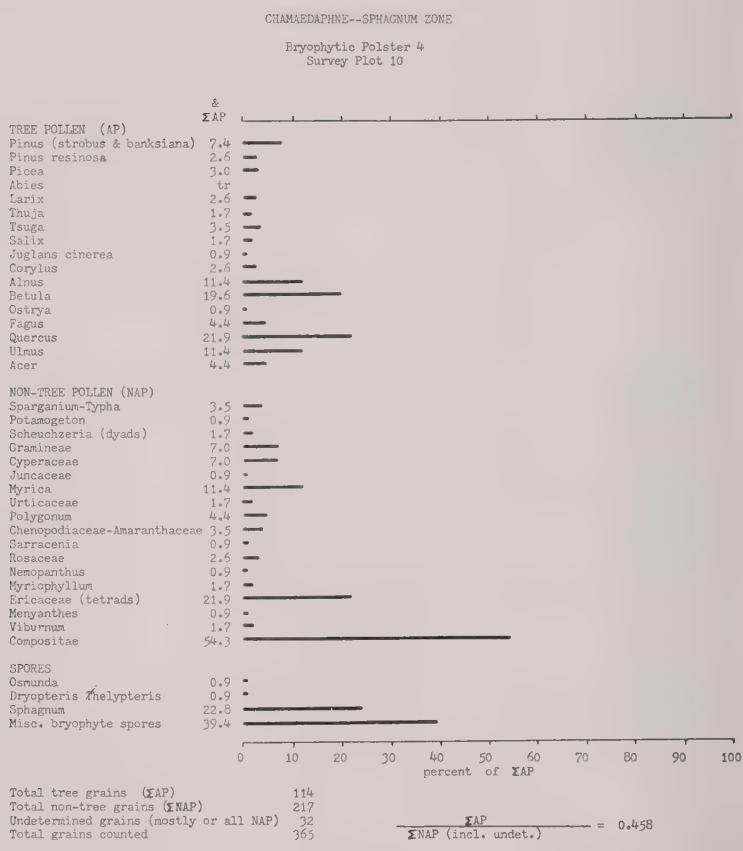

FIG. 5. Pollen spectrum of Bryophytic Polster No. 4 collected on Vegetation Survey Plot 10 in the *Chamaedaphne-Sphagnum* Zone.

DISCUSSION

Evaluation of the pollen spectra must take into consideration the fact that certain plants, primarily the anemophilous species, produce much greater amounts of pollen than others. *Quercus, Pinus, Alnus, Betula, Corylus, Ulmus,* and the Gramineae are such outstanding producers, as are also certain of the Compositae, especially those that are anemophilous. The pollen of trees is more likely to be distributed

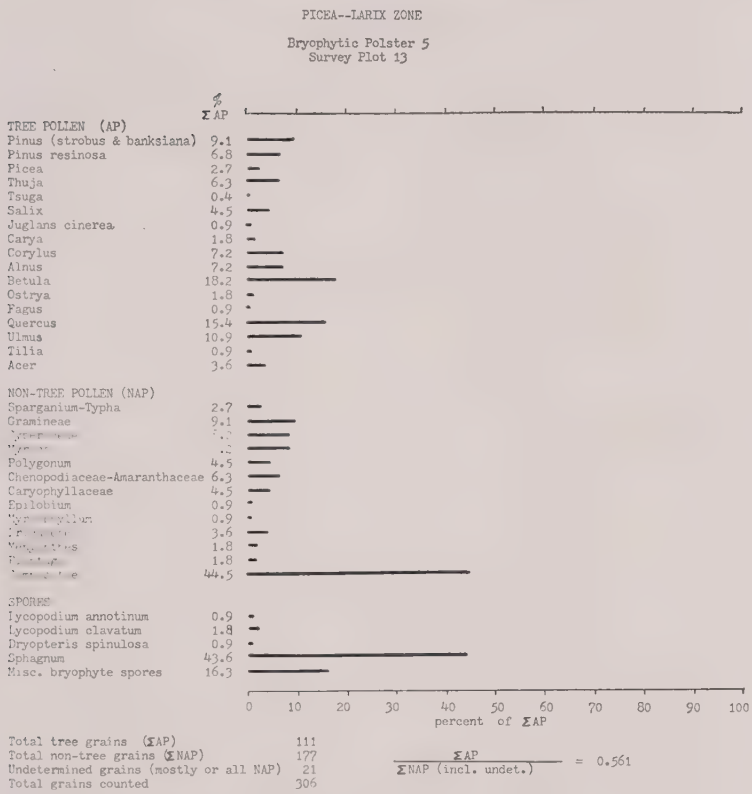

FIG. 6. Pollen spectrum of Bryophytic Polster No. 5 collected on Vegetation Survey Plot 13 in the *Picea-Larix* Zone.

greater distances by reason of being launched higher above the ground and in faster air currents. The lower the stature of the plant, the less opportunity its pollen will have for long-range transport by wind. Therefore, the tree component of the pollen rain on a given site tends to represent a more extensive sample of vegetation than the shrub and herb components.

The pollen spectra shown in Figures 2 through 8 may be compared with the respective phytosociological lists in Tables I through VII to evaluate the representativeness of the pollen rain for a given station

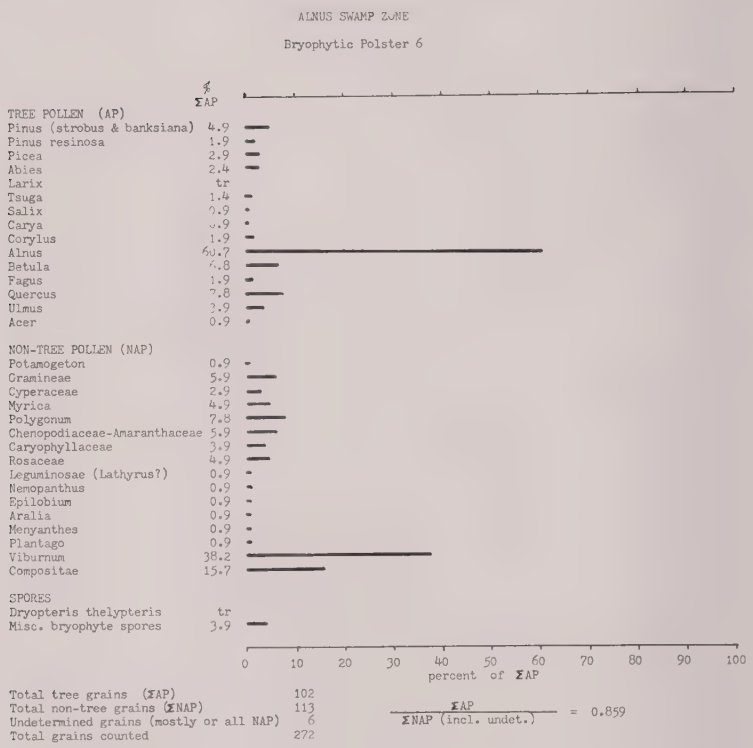

FIG. 7. Pollen spectrum of Bryophytic Polster No. 6 collected in the *Alnus* Swamp.

The pollen values for *Pinus, Tsuga, Ostrya, Fagus, Quercus, Ulmus, Tilia,* and *Fraxinus* undoubtedly represent the regional pollen rain (i.e., an area with a radius of several miles from the site sampled). Pollen of *Picea, Abies, Alnus, Betula,* and *Acer* is probably in part the regional component, but certainly in part from trees on the bog and in the *Thuja* Swamp. *Juglans cinerea* and *Carya* pollen may represent elements of "long-range drift" in the pollen rain, as these trees are not recorded for Emmet and Cheboygan counties in the natural vegetation (Voss, 1954). On the other hand, these two pollen types may have come from the few trees of these genera present as house plantings in the general area (E. G. Voss, personal communication).

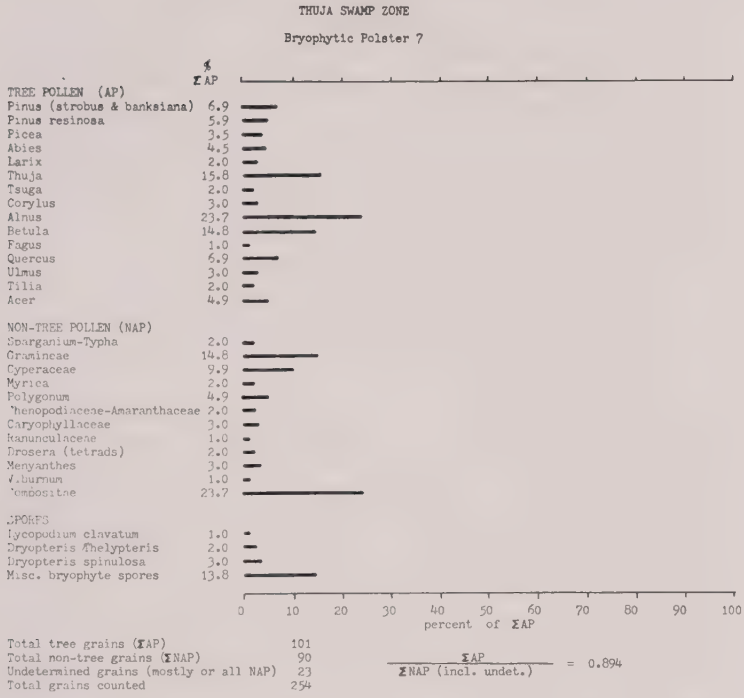

FIG. 8. Pollen spectrum of Bryophytic Polster No. 7 collected in the *Thuja* Swamp.

The *Larix* pollen is probably derived exclusively from trees on the bog, and the *Thuja* pollen exclusively from trees in the *Thuja* Swamp. A characteristic of the regional pollen components (e.g., *Quercus* and *Fagus*) is that the percentages vary more or less as a group from one polster sample to another, whereas the pollen types that are of local origin (e.g., *Thuja*) vary with the location of the sample over small distances. Pollen types with both regional and local components in the pollen rain (e.g., *Picea* and *Alnus*) have a relatively constant minimum percentage from one station to another, but show locally marked increases. Long-range drift components and regional flora elements that are present in small numbers or are small producers of pollen are erratic in their appearance in pollen spectra. *Carya* and *Juglans*

cinerea produce moderate quantities of pollen, but it is difficult to determine in this instance what the source of the pollen might have been. *Tilia* is a relatively smaller producer of pollen and is commonly underrepresented in pollen spectra.

The Gramineae and Compositae are virtually absent from the bog and the *Thuja* Swamp. Their large representation must be entirely from regional pollen rain. The region has extensive areas of fields, pastures, and fallow ground, as well as weedy roadsides that are rich in grasses and composites. Almost half of the pollen grains of the Gramineae were found to be relatively large (more than 40 μ in diameter) like those of cultivated cereal grasses. The Chenopodiaceae-Amaranthaceae pollen probably comes from weed species on cultivated or disturbed ground.

The Cyperaceae is represented with relative accuracy in proportion to its very local occurrence. The Ericaceae, however, is greatly underrepresented in most of the spectra. The extreme underrepresentation in the spectrum of Polster No. 6 may be a result of the fact that the Ericaceae in the vicinity of Plot 13 appeared to produce relatively few inflorescences, and the bog surface was dry, conditions operating against the production and preservation of pollen.

Some bog plants are definitely present nearby when their pollen appears in the spectrum, for example, *Scheuchzeria, Drosera, Sarracenia*, and *Sphagnum*. These same plants, however, may be present in large numbers without appearing in the corresponding pollen spectrum. Another group of bog and aquatic plants, *Typha, Potamogeton, Sagittaria, Myrica, Myriophyllum, Dryopteris thelypteris*, and *Polygonum*, appear to have their pollen and spores distributed widely over the bog area, but probably not as widely as the regional component of the pollen rain.

Some grains that appear in the spectra are difficult to appraise, for example, *Plantago*, the species of *Lycopodium*, and *Osmunda*; but most likely they belong to the regional component of the pollen rain. The erratic occurrence of the miscellaneous bryophyte spores is also difficult to evaluate, although this could be a result of intermittent fruiting periods.

It is interesting to compare the spectra from these bryophytic polsters with the uppermost level in Sears' (1942) pollen diagram from the peats in Inverness Mud Lake Bog. Only the tree components of the fossil pollen were presented in his profile, and the precise percent-

ages were not shown; but from the profile diagram one can see that the pollen types were ranked as follows (in order of decreasing abundance): *Pinus, Tsuga,* Betulaceae, *Picea, Fagus,* and *Quercus. Abies* was not present above the two-foot depth, and *Salix* was not present above the three-foot depth. In contrast, the bryophytic polster spectra show *Quercus* equaling or exceeding *Pinus, Tsuga* much less abundant, and *Abies* present in all but one polster. This difference between the top of the profile of fossil pollen and the modern spectra may have significance with respect to vegetational change over the past 100 years. Pine (*Pinus*) and hemlock (*Tsuga*) have been logged out of the forests and have been destroyed by fires. Oak (*Quercus*) and balsam fir (*Abies*) are prominent in second-growth forest and old field successions, respectively.

In the pollen diagram from Douglas Lake, Cheboygan County, published by Wilson and Potzger (1943), the following approximate percentages for the pollen can be read from the diagram: *Pinus*, 45%; *Betula*, 18%; *Tsuga*, 8%; *Abies*, 8%; *Quercus*, 5%; *Fagus*, 8%; *Larix*, 3%; *Acer*, 2%; *Ulmus*, 1%; *Salix*, 1%. This spectrum is similar to that of Sears for the uppermost level in the Inverness Mud Lake profile, except for the presence of *Abies, Larix, Acer, Ulmus,* and *Salix,* and the absence of *Picea.* But again the predominance of *Pinus* and *Tsuga* over *Quercus* and the larger proportion of *Fagus* is in contrast with the modern spectra from the bryophytic polsters examined in this study.

Conclusions

This study of pollen spectra from seven bryophytic polsters collected in Inverness Mud Lake Bog provides some guidance in the interpretation of pollen profiles from the region, especially with respect to NAP, when such more detailed pollen profiles are available. The regional vegetation indicators are the pollen of *Pinus, Quercus, Fagus, Tsuga, Acer,* Gramineae, and Compositae. Regional indicators which are influenced by local bog or swamp stands of the same entities are *Picea, Betula,* and *Abies.*

Reliable indicators of local vegetation are Cyperaceae, Ericaceae, and *Thuja*; if one of these is present in the pollen spectrum, the contributing plants were growing essentially on that site. Other indicators of local vegetation are less reliable; if the pollen occurs in the spectrum, the contributing plants were probably within a few hundred

yards of the depositing area. These include *Larix, Thuja, Scheuchzeria, Epilobium, Potamogeton, Typha, Sparganium, Sarracenia, Drosera, Myriophyllum, Viburnum, Dryopteris thelypteris,* and *Sphagnum.*

Many other entities in the pollen spectra of these bryophytic polsters remain to be explained with respect to their representativeness.

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PHYTOSOCIOLOGICAL STUDY OF INVERNESS MUD LAKE BOG, CHEBOYGAN COUNTY, MICHIGAN[1]

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Inverness Mud Lake, a relic bog formation occurring in the transitional region between the coniferous forest to the north and the deciduous forests on the south, has been the subject of several floral and ecological investigations in the past. These studies of Coe, Erickson, and Woollett (1924) and of Gates (1942) contain only species lists of the vascular plants occurring in the area and mention brief descriptions of the vegetation features. Therefore, the major objectives of this investigation were to evaluate quantitatively the vegetation composition and structural relationships of the various plant communities comprising the Mud Lake area; and to utilize the methods of the Zurich-Montpellier School of Phytosociology for this evaluation. Three ecologically distinct communities occurring along the southeast margin of the lake were studied: the *Thuja* seepage, the *Sphagnum* bog extending east from an ice-push ridge near the lake margin, and the quaking *Carex* mat bordering the open water of the lake (Fig. 1).

Description of the Area

Inverness Mud Lake (herein spoken of as Mud Lake) lies within the upper extension of the Carp River drainage basin. This basin projects an arm into the northwest corner of Inverness Township, Cheboygan County, Michigan, and contains Mud Lake. The geo-

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graphic placement of the area is: T37N, R2W, in parts of Sections 7 and 18.

Cheboygan County, situated at the apex of the northern lower peninsula of Michigan, lies between Lake Michigan to the west and Lake Huron to the east. The area is characterized by late Pleistocene glacial features; namely, glacial lake basins, meltwater valleys, drumlins, ridges, and channeled ground moraines (Spurr and Zumberg, 1956). The principal topographic features are orientated from northwest to southeast corresponding with the direction of ice movement.

The open water of Mud Lake is one fifth of a mile wide and slightly more than twice as long (Fig. 1). An additional 300-foot area of sedge mat is situated at the southeast corner of the lake. This represents a threefold increase from the 1925 mat boundary (Coe, et al.). These same authors report the lake as distinctly alkaline (from 7.0 to 8.0 in pH), "... While the surrounding mat is decidedly

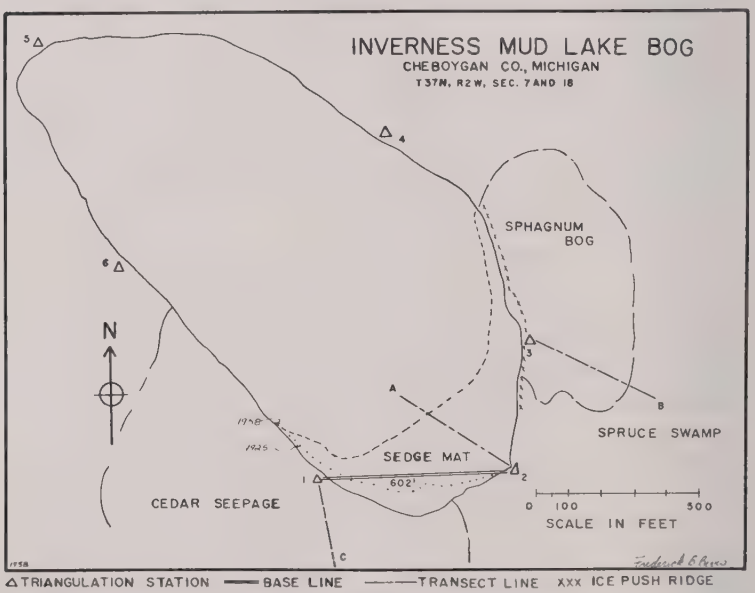

Fig. 1. Map showing the three ecologically distinct communities along the southeast margin of Inverness Mud Lake Bog.

acid." Field readings taken in August of this study show the pH at various stations was: 6.4 in the flocculent mud extending into the open water from the sedge mat; varying from 5.1 to 6.2 on the outer edge of the mat; dropping to 4.0 on the mat proper; varying from 3.8 to 4.4 on the *Sphagnum* bog; and from 6.0 to 6.5 under the heavy growth of *Thuja*.

The only perceptible flow of water into the lake is through the *Thuja* seepage. Here the water table is perched above a sand subsoil lying only two feet below the ground surface. In a few locations the water flowage can be seen through the entangled mass of cedar roots.

In concluding this brief description of the area a few comments on the prevailing climatic conditions are necessary. The climate of the northern lower peninsula of Michigan is largely controlled by three factors: proximity to both Lake Michigan and Lake Huron; the local topography; and the existing vegetation patterns. Local extremes of climate, resulting from the interaction of these features, are characteristic of the area.

Picea mariana (Black Spruce) and other northern coniferous species find suitable habitat primarily in wet lowland areas associated with poor to moderate drainage systems and having thick accumulations of organic materials. The occurrence of these relic species and communities, notably the conifer swamps and *Sphagnum* bogs of the Lake States region, are definite indicators of cooler climates during the past. Relic communities persist in local areas not characterized by the present regional climatic regime. Cain (1944) has remarked, ". . . relic colonies [occur] in local situations where frequently edaphic or microclimatic conditions provide at least temporary compensation for a general climatic unfavorableness."

Methods of Study

Transect lines were placed through the three communities and a series of milacre plots (approximately 2 m. on a side) were marked out 2 m. apart on alternate sides of the transect line. In this way a total of 90 plots was established: 30 in the *Thuja*; 40 in the *Sphagnum*; and 20 covering the *Carex* mat. A total area of 120 square meters in the *Thuja*, 160 in the *Sphagnum*, and 80 in the *Carex* community was studied. Each series of plots was tied into a triangulation station located on the base map of the area (Fig. 1).

TABLE I

Sociability Scale (after Braun-Blanquet, 1932)

5	Plants occurring in great crowds (pure populations)
4	Plants in small colonies, in extensive patches, or forming carpets
3	Plants in groups, in small patches, or in cushions
2	Plants in small groups or tufted
1	Plants growing in one place; singly, solitarily

TABLE II

Combined Cover-Abundance Scale (Braun-Blanquet, 1932)

5	76–100% cover of the plot regardless of the number of plants
4	51–75% cover of the plot regardless of the number of plants
3	26–50% cover of the plot regardless of the number of plants
2	5–25% cover; individual plants common, but low in cover value
1	Less than 5% cover; plants abundant but of insignificant value
+	Less than 1% cover; plants occasional
r	Erratic occurrence; usually one plant on a plot

A plane table survey was conducted around the lake, and the various vegetation patterns immediately surrounding the open water were plotted. Detailed presentation of these vegetational features will follow in the discussion of the phytosociological survey.

The methods of vegetation analysis developed by the Zurich-Montpellier School were utilized in the recording of plot data (see Becking, 1957). Three basic concepts were used; Sociability (Table I), Cover Abundance (Table II), and Carles (1948) system of importance values.

Relative importance (RI) is based on the values obtained in the cover-abundance determinations and reflects the plant's dominance in the community in terms of its number of individuals, their degree of distribution, and their total coverage. The importance scale is as follows: a cover-abundance value of 5 equals 80; one of 4 is 60; 3 is 40; 2 is 20; 1 is 5; + equals 0.1; and r has no value (is 0). The RI values for each species were obtained by totaling the importance scale figure of each cover-abundance number and dividing by the total number of plots in the community. These values were used to facilitate the comparison of the synusiae, to determine the dominant,

TABLE III

Life-Form Classification (after Raunkier, 1934)

E	Epiphytes
MM	Mega and meso-phanerophytes (more than 24 feet tall and having exposed overwintering buds)
M	Micro-phanerophytes (6 to 24 feet tall with exposed buds)
N	Nano-phanerophytes (less than 6 feet tall)
Ch	Chamaephytes (less than 25 cm. tall; buds protected just above the ground surface)
H	Hemicryptophytes (buds at the ground level)
G	Geophytes (buds overwintering in the soil)
HH	Hydrophytes (aquatic plants)
Th	Therophytes (annual seed producers)

co-dominant, and character species of a community, and to compare the vegetation structure and composition between the communities.

The frequency concept (per cent occurrence of a species from all the sample plots) and Raunkier's (1934) system of plant life-form expressions (Table III) were utilized to depict the position of the individual species within the community.

Phytosociological Survey

The value of any vegetation investigation depends to a great extent on the accuracy of the method employed and on the degree of unbiased judgment achieved by the observer. The Zurich-Montpellier method largely eliminates the errors of judgment that often result when a high degree of precision is attempted by ocular estimation. Numerical classes are large enough to include the limits of error involved.

Phytosociology does not attempt to analyze the relationships of the individual plant to its environment, nor to study one particular environmental factor, but, more specifically, it confines itself to the study of the plant community. Becking (1957) states that phytosociology studies include "all characteristics of plant communities . . . , their physiognomy, floristic composition, community morphology and structure, community development and change, the multilateral relations of plants to one another and to environment, and the classification of communities." In contrast to general "plant ecology," phytosociology is the science of community relations (i.e., the study of the phytocenose).

Cajander (1903) was the first to introduce the tabulation of plot data by numerical means. At present, practically all aspects of the community are approached by some numerical evaluation; such as, its fidelity, cover abundance, sociability, frequency, constancy, relative importance, and presence. Each species in the communities studied is listed on the Vegetation Plot Data Sheet (Tables IV, V,

TABLE IV

VEGETATION PLOT DATA SHEET—INVERNESS MUD LAKE BOG, CHEBOYGAN COUNTY, MICHIGAN

Community: THUJA SEEPAGE Transect: C Plots: 1 to 30 Total Area: 120 sq. m.

	Life-Form, Species	F	C-A.S.	RI
	TREE STRATUM Height: 20 to 90 ft., Crown Closure: 80%			
MM	Thuja occidentalis	57	4.1	20.0
MM	Abies balsamea	22	1.1	6.2
MM	Acer rubrum	17	1.1	6.0
MM	Betula allegheniensis	3	r.1	0.7
MM	Picea mariana	3	r.1	1.3
	SHRUB STRATUM Height: to 9 ft., Total Cover: 15%			
Ch	Taxus canadensis	30	2.3	19.3
M	Acer spicatum	33	1.1	8.8
N	Amelanchier spp.	10	r.1	4.0
	HERB STRATUM Height: 2 in. to 18 in., Total Cover: 35%			
H	Coptis groenlandica	65	2.3	12.5
H	Rubus pubescens	23	1.2	6.7
G	Aralia nudicaulis	27	1.1	5.3
G	Maianthemum canadense	17	1.1	4.2
H	Galium aparine	20	1.2	4.0
Ch	Linnaea borealis	13	+.1	1.5
H	Trientalis borealis	17	+.1	3.3
H	Clintonia borealis	13	+.1	4.5
G	Athyrium filix-femina	13	+.3	2.6
G	Goodyera repens	10	r.1	+
Ch	Pyrola rotundifolia	7	r.1	0.8
Ch	Mitchella repens	3	r.1	+
G	Habenaria hyberborea	3	r.1	+
	HERB STRATUM (*Continued*)			
G	Dryopteris spinulosa	3	r.1	+
G	Erythronium americanum	3	r.1	+
G	Dryopteris marginalis	3	r.1	+
	MOSS (GROUND) STRATUM Height: to 2 in., Total Cover: 15%			
Ch	Mnium punctatum var. elatum	17	1.5	8.6
Ch	Mnium punctatum	7	+.4	4.0
Ch	Thuidium recognitum	14	+.5	2.9
Ch	Thuidium delicatulum	14	+.5	4.0
Ch	Sphagnum magellanicum	10	+.5	4.0
Ch	Sphagnum wulfianum	10	+.5	4.7
E	Bazzania trilobata	17	+.5	4.0
E	Radula complanata	20	+.4	3.2
E	Cladonia cristatella	3	r.1	+
E	Parmelia sulcata	3	r.1	+
E	Parmelia rudecta	3	r.1	+
E	Parmelia physodes	3	r.1	+
E	Bacidia muscorum	3	r.1	+
E	Usnea florida	3	r.1	+
E	Cetraria saepincola	3	r.1	+
Ch	Heterophyllum haldanianum	3	r.1	+
**	Dicranum rugosum, Hypnum pratense, Calliergon cordifolium, C. stramineum, Pellia epiphylla, Phlyctis agelaea, Cephalozia connivens, Riccardia latifrons, and Lophocolea heterophylla.			

KEY: F = Frequency of Occurrence on Plots (%).
C-A.S. = Cover-Abundance, Sociability Values.
RI = Relative Importance Value.
+ (RI) = RI values less than 0.1.
** Collections made of these species in the moss stratum, no values assigned.

TABLE V

VEGETATION PLOT DATA SHEET—INVERNESS MUD LAKE BOG, CHEBOYGAN COUNTY, MICHIGAN

Community: SPHAGNUM BOG Transect: B Plots: 31 to 70
Total Area: 160 sq. meters

Life-Form, Species	F	C-A.S.	RI
TREE STRATUM Height: 4 to 35 ft., Crown Closure: 2%			
MM Picea mariana	10	1.1	4.5
MM Larix laricina	8	+.1	3.0
SHRUB STRATUM Height: to 24 ft., Total Cover: 20%			
Ch Kalmia polifolia	25	2.2	12.0
Ch Andromeda glaucophylla	20	1.2	5.8
Ch Ledum groenlandicum	13	+.2	3.1
N Vaccinium macrocarpum	8	+.4	3.0
N Picea mariana	5	+.1	2.5
N Chamaedaphne calyculata	3	r.4	1.5
N Vaccinium oxycoccos	13	r.3	0.5
HERB STRATUM Height: 2 in. to 1 ft., Total Cover: 20%			
H Rhynchospora alba	50	+.1	0.4
G Smilacina trifolia	20	+.1	0.6
HH Drosera rotundifolia	13	+.1	0.5
G Habenaria bleparioglottis	10	r.1	0.3
HH Menyanthes trifoliata	8	+.1	0.1
HH Nymphaea odorata	3	r.1	1.0
H Carex pauciflora	5	r.1	0.1
G Arethusa bulbosa	8	+.1	+
HH Sarracenia purpurea	8	r.1	+
H Eriophorum viridi-carinatum	8	+.1	+
HERB STRATUM (*Continued*)			
HH Potentilla palustris	5	r.1	+
H Carex lasiocarpa	5	r.1	+
G Pogonia ophioglossoides	3	r.1	+
Ch Pyrola virens	3	r.1	+
HH Drosera intermedia	3	r.1	+
HH Drosera linearis	3	r.1	+
H Viola pallens	3	r.1	+
G Cypripedium acaule	3	r.1	+
H Carex oligosperma	3	r.1	+
E Arceuthobium pusillum	10	+.1	+
HH Caltha palustris	5	r.1	0.1
MOSS (GROUND) STRATUM Height: to 2 in., Total Cover: 25%			
Ch Sphagnum magellanicum	70	2.5	27.5
Ch Sphagnum warnstorfianum	55	1.5	6.5
Ch Sphagnum cuspidatum	30	+.5	0.3
Ch Sphagnum teres and S. subsecundum	28	+.5	0.3
Ch Sphagnum capillaceum	15	r.5	+
Ch Dicranum bergeri	5	r.5	+
Ch Tetraphis pellucida	3	r.5	+
** Sphagnum papillosum, S. girgensohnii, Microlepidozia setacea, Mylia anomala, Porella platyphylloidea, Lejeunea cavifolia, Alectoria nidulifera, Parmelia olivacea, Cetraria ciliaris, C. saepincola, Cephalozia pleniceps.			

KEY: F = Frequency of Occurrence on Plots (%).
C-A.S. = Cover-Abundance, Sociability Scale.
RI = Relative Importance Values.
+ (RI) = value less than 0.1.
** = Collections made, no assigned values.

and VI) according to its occurrence in the various strata (synusiae) of the community. Life-form values, frequency of occurrence percentages, cover-abundance and sociability figures, and relative importance values are presented. The cover-abundance and sociability, as well as the relative importance figures are based on the average

TABLE VI

VEGETATION PLOT DATA SHEET-INVERNESS MUD LAKE BOG, CHEBOYGAN COUNTY, MICHIGAN

Community: CAREX MAT Transect: A Plots: 71 to 90 Total Area: 80 sq. meters

Life-Form, Species	F	C-A.S.	RI
TREE STRATUM—Absent			
SHRUB STRATUM			
Height: 3 to 20 ft., Total Cover: 1%			
N Alnus (incana-rugosa)	5	+.3	3.0
N Salix spp.	5	+.4	2.0
N Nemopanthus mucronata	5	r.2	0.2
N Chamaedaphne calyculata	5	r.3	+
HERB STRATUM			
Height: 2 in. to 3 ft., Total Cover: 60%			
H Carex lasiocarpa	75	3.5	40.0
H Eleocharis olivacea	15	+.2	2.2
H Scirpus cyperinus	15	+.2	1.5
H Carex comosa	15	+.3	1.0
H Dulichium arundinaceum	15	r.2	0.5
G Hypericum virginicum	15	r.1	0.3
H Lycopus virginicus	15	r.2	0.3
HERB STRATUM (*Continued*)			
HH Nymphaea odorata	5	r.2	+
H Carex chordorhiza	10	r.2	+
H Eriophorum virginicum and E. gracile	10	r.2	+
H Epilobium strictum	5	r.1	+
HH Calla palustris	5	r.4	+
H Carex canescens	5	r.2	+
HH Nuphar advena	5	r.2	+
H Galium palustre	5	r.1	+
HH Hypericum boreale	5	r.1	+
H Scheuchzeria palustris		**	
H Carex disperma		**	
H Carex trisperma		**	
MOSS (GROUND) STRATUM			
Height: to 2 in., Total Cover: 5%			
HH Drepanocladus exannulatus	15	+.5	0.5
HH Calliergonella cuspidata	5	r.3	+
H Cladopodiella fluitans		**	

KEY: F = Frequency of Occurrence on Plots (%).
C-A.S. = Cover-Abundance, Sociability Value.
RI = Relative Importance Values.
+ (RI) = value less than 0.1.
** = Collections made, no assigned values.

value obtained in the summation of the respective values from each plot. The figures represent the value of a species over the total sample area of the community.

DISCUSSION

Synusial formation is a distinctive feature of the *Thuja* seepage, whereas in the *Carex* and *Sphagnum* communities, the development of characteristic belts of vegetation is most pronounced. By accepting the assumption that a forest cover is the ultimate vegetation growth that will occupy wild land areas of the Lake States region, the lack of synusial development serves to illustrate the young succes-

TABLE VII

TOTAL RELATIVE IMPORTANCE

Stratum	Communities		
	Thuja	*Sphagnum*	*Carex*
Tree	34.1	7.5	—
Shrub	32.1	28.4	5.2
Herb	46.4	3.1	45.8
Moss	35.4	34.6	0.5

sional character of the latter communities. In contrast, the *Thuja* seepage stands at a more advanced successional position, showing definite synusial structure.

Total relative importance values (TRI) are extremely useful in the evaluation of community structure (Table VII). These values are obtained by summing the RI values for each species as they occur in their respective strata.

The *Carex* community is dominated by the herb stratum with *Carex lasiocarpa* having an RI value of 40.0 in relation to the stratum's TRI of 45.8. The *Sphagnum* community has a dominant moss stratum and also a distinctive heath-shrub layer. *Sphagnum magellanicum* with a RI value of 27.5 from a TRI of 34.6 is an important feature of the community. *Kalmia polifolia* (RI of 12.0) occupies a dominant place in the low shrub synusiae.

The belts of vegetation in the *Carex* and *Sphagnum* areas show considerable stability in their space-age relationships. Each belt (including the Black Spruce islands) was found to have persisted for a relatively long time and had maintained similar vegetative composition for its duration. Cuttings made through the submerged stems of *Chamaedaphne calyculata*, growing between the water-moat and ice-push ridge separating the *Carex* quaking mat from the *Sphagnum* bog, showed 50 or more yearly rings. This *Chamaedaphne* belt extended along the inner edge of the *Carex* mat, being replaced in a few places by patches of *Alnus incana*.

Several increment core measurements of 115 years and 124 years were taken from Black Spruce growing on the ice-push ridge. These ages show that this spruce belt has persisted for a long time and further substantiates the idea of stability and duration of the vegetative

belts. *Tetraphis pellucida*, a moss usually found growing on advanced stages of decaying wood, occurs on spruce and *Larix laricina* logs along the ridge.

A wide area of open *Sphagnum* bog stretches from the spruce belt on the ridge to the Black Spruce swamp east of Mud Lake. This flora has close affinities to the boreal bog elements on Isle Royale, Michigan (Adams, 1909; Brown, 1933), and to those of eastern Canada (Dansereau and Segadas-Vianna, 1952). Species lists vary little in these regions; the only change in vegetation readily observable are those differences in cover abundance and, therefore, the RI values that would be determined for the species. These changes may be the result of differences in micro-habitat conditions or from the successional stage of the bog.

In several points on the Sphagnum bog, the ground water level intercepts the vegetative cover, forming small moist depressions. The occurrence of *Sphagnum teres, S. capillaceum, S. papillosum*, and *S. girgensohnii*, as well as *Drosera rotundifolia, Smilacina trifolia*, and *Kalmia polifolia* are closely associated and often restricted to these water-filled depressions. At the other extreme, *Sphagnum warnstorfianum* and *Andromeda glaucophylla* were usually found forming raised hummocks over the bog. *Sphagnum magellanicum*, the dominant species in the community, forms a continuous level carpet over much of the area. Interspersed on this moss carpet were *Rhynchospora alba* and *Habenaria blephariglottis*, and trailing over it were *Vaccinium macrocarpon* and *V. oxycoccos*. The Rhynchospora has a frequency of 50 per cent, but a cover-abundance value of only +.1 and an RI of 0.4. It is a character species of the community with only relatively minor importance.

In the transitional area between the exposed *Sphagnum* bog and the spruce swamp occur islands of spruce and larch surrounded by typical bog vegetation structure. Ages of two Black Spruce from an island were 150 and 200 years; the age of a larch was approximately 200 years. The diameter of these trees showed their abnormally slow growth, ranging from four inches for the larch to six inches for the largest of the spruce. The heights of these trees were 12, 22, and 35 feet, respectively.

The structure of these islands differed considerably from the adjacent bog, both in species composition and synusial development. A representative bog and spruce-larch island plot are compared in Ta-

TABLE VIII

COMPARISON OF A SPHAGNUM BOG AND SPRUCE ISLAND PLOT

Stratum / Species	Sphagnum No. 6 C-A.S.	Sphagnum No. 6 RI	Spruce No. 9* C-A.S.	Spruce No. 9* RI
Tree				
Picea mariana			3.2	40
Larix laricina			3.1	40
Shrub				
Kalmia polifolia	r.1	0	2.2	20
Herb				
Smilacina trifolia	1.1	5		
Habenaria blephariglottis	1.1	5		
Rhynchospora alba	+.1	0.1		
Drosera rotundifolia	+.1	0.1		
Pyrola virens			r.1	0
Viola pallens			r.1	0
Moss				
Sphagnum magellanicum	3.5	40	1.5	5
S. warnstorfianum	1.5	5		
S. cuspidatum	+.5	0.1		
S. teres & capillaceum	+.5	0.1		
S. subsecundum			+.5	0.1

* Lichens growing on the Spruce were: *Cetraria saepincola*, *Cetraria ciliaris*, *Alectoria nidulifera*, and *Parmelia olivacea*. Bryophytes present in the spruce plot but not in the *Sphagnum* were: *Microlepidozia setacea*, *Mylia anomala*, *Porella platyphylloidea*, *Lejeunea cavifolia*, *Dicranum bergeri*, and *Cephalozia pleniceps*. Dicranum and Microlepidozia were found only at the base of spruce, protected by the overhanging branches.

ble VIII. The differences in cover abundance and sociability, relative importance, and synusiae are striking.

Before continuing with a discussion of the structure of the *Carex* mat vegetation, a profile through the peat formation of the *Sphagnum* bog is described. From the bog surface to a depth of nine feet, *Sphagnum* peat in various stages of decomposition is present. Lenses of decaying spruce and larch logs are scattered in the same region. A gelatinous deposit occurs at nine feet and continues to about eleven feet. At this position a distinct marl accumulation is present and

at thirteen feet sandy lake bottom sediments occur. Many kinds of shells were in these sandy bottom layers (see also Gates, 1942).

On the *Carex* mat two wide belts of vegetation were present; one of *Carex lasiocarpa* on the stable inner mat, and the other of *Eleocharis olivacea* on the outer area of gelatinous mud. *Dulichium arundinaceum*, the three-way-sedge, occurred in patches on the more solid portions of the Eleocharis belt, while *Carex comosa* occurred in small clumps between the two areas. *Drepanocladus exannulatus* and *Calliergonella cuspidata* were found bordering small water-filled depressions and along muskrat runways in the mat. Additional species listed on the community table (Table VI) were found scattered through the thick mat of *Carex lasiocarpa*.

The similarities in TRI values for each stratum in the *Thuja* seepage community (Table VII) are notable. The dominant tree member is *Thuja occidentalis* (RI of 20.0), while *Abies balsamea* (RI of 6.2) and *Acer rubrum* (RI of 6.0) can be considered as co-dominants. The entangled mass of exposed *Thuja* roots, the proximity of the water table, and the rich accumulation of organic materials, all combine to form a diversity of suitable micro-habitats for the herb and moss synusiae.

Plant distribution patterns in the *Thuja* do not show distinctive belts of vegetation. Rather species occurrence in the lower synusial layers are restricted by the location and suitability of the habitat. *Taxus canadensis* and *Acer spicatum*, the dominant and characteristic members of the shrub layer, occur on the drier sites. There was little development of herbaceous or bryophytic cover under the *Taxus*, possibly because these thick clumps excluded almost all sunlight. *Coptis groenlandica*, the most abundant species in the herb layer, *Maianthemum canadense*, *Pyrola rotundifolia*, and *Linnaea borealis* were found growing in moist areas at the base of large *Thuja*. *Clintonia borealis*, *Trientalis borealis*, and *Rubus pubescens* were more restricted in distribution to the hummocks of *Sphagnum magellanicum* and *S. wulfianum*, while *Mnium punctatum* var. *elatum* was confined to moist low hollows. Both the liverworts, *Bazzania trilobata* and *Radula complanata* were associated with the moist, protected, lower trunks of *Thuja*.

Because of the nature of previous floral and ecological work at Mud Lake, there can be no quantitative comparison of data. There-

fore, only a limited discussion of general changes in the vegetation will be presented.

Coe, Erickson, and Woollett (*ibid.*) report the presence of an Iris-Aspidium and Chamaedaphne "association" in conjunction with the *Carex* mat. The leatherleaf (Chamaedaphne) association at this time covered a more extensive area lying between the ice-push ridge and the sedge mat and was also a prominent feature in the *Sphagnum* bog. Now, leatherleaf is confined to the border of a few spruce islands, along the eastern margin of the *Sphagnum* bog near the spruce swamp, and in the narrow belt along the water moat on the inner edge of the *Carex* mat. The Iris-Aspidium "association" is no longer present.

At the time of their study (Coe, et al.), mat development was limited to the extreme southeast corner of the lake. The present mat occupies a much greater area (Fig. 1). Gates (*ibid.*) has a photograph of this area taken in 1939 which shows the presence of clumps of vegetation over the Eleocharis belt. He states, "Since neither the *Carex lasiocarpa* nor the Chamaedaphne associations appear to invade the *Eleocharis olivacea* association on this soft organic mud, its successional relationships are not yet clear." *Dulichium arundinaceum* and *Carex comosa* (or a similar clump-forming sedge) are readily identified in this illustration; in all probability these species help form a more suitable substrate for the invasion of *Carex lasiocarpa*. This species appears to become established after early successional species have helped to stabilize marginal areas of the existing mat and the gelatinous mud area. The presence of *Menyanthes trifoliata, Potentilla palustris,* and *Nuphar* pushing out into the mud along the edge of the sedge mat could also aid in preparing a firm base for the extension of the *Carex lasiocarpa*. Perhaps the most prominent successional feature of Mud Lake is the speed by which the sedge mat has enlarged.

Only a few obvious changes in the *Sphagnum* bog community will be noted. The absence of leatherleaf has previously been discussed. A marked decrease in the abundance of *Larix* bears further comment. Few seed trees survived the larch sawfly outbreaks in Michigan during the 1920's (Graham, 1956). Gates (*ibid.*) states tamarack was a dominant tree in the Mud Lake area in 1916, and Coe (Coe, et al.) maps a large distribution in 1924. Today, a few old-aged,

poorly developed trees exist in the protected islands of spruce and in the transitional region between the *Thuja* seepage and the Black Spruce swamp, and have a low cover-abundance and relative importance rating (Table V). Further phytosociological study of Mud Lake will aid in the analysis of vegetation pattern, composition, and structure and will thereby disclose successional trends not completely understood.

Summary

The validity and therefore importance of any ecological method rests on its ability to provide an intellectually satisfying account of the factors involved in the structure, function, and history of vegetation formations. The phytosociological approach to vegetation measurement allows extreme flexibility in its analyses of the community complex and offers an opportunity to rapidly compare vegetation on a regional basis.

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EFFECT OF SETTLEMENT ON THE VEGETATION OF THE UNIVERSITY OF MICHIGAN BIOLOGICAL STATION[1]

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The University of Michigan Biological Station, situated between Douglas and Burt lakes in Cheboygan County, Michigan, is one of the most intensively studied ecological areas in the state. Although the effect of settlement during the past century, accompanied by severe forest and logging fires, is known in general terms, yet the precise vegetational history of any particular area in the county is not at all known. Without this information, the investigator is often severely handicapped, both in understanding how present conditions came to be and in predicting what course future changes will take. This paper lists and discusses several new facts that contribute to a more thorough and precise knowledge of this recent vegetational history.

No study of the fire and logging history has ever been made at the Station, nor have the references to these treatments ever been compiled. Most of the major ecological papers are cited by Voss (1956), including the important papers by the early ecologists F. C. Gates and H. A. Gleason. Several of these mention logging and fire, but too few of them record their precise dates, locations, and extent. Donahue (1936) claims the pine land was logged in 1871–72 and the hardwoods in 1912 but does not mention the source of his information. Both dates are reasonable although this paper reports evidence which shows that the pine logging occurred almost ten years later.

Voss (1956) discusses much of the flavor and history of the settlement of the county. Table I gives several county statistics and summarizes the progression of settlement. It is within the framework of these events that the logging, burning, and settlement of the Biological Station took place. The county was formed and the

[1] Contribution from the Biological Station of The University of Michigan.

TABLE I

SAWMILL PRODUCTION, FARM AREA, AND POPULATION CHANGE, CHEBOYGAN COUNTY, MICHIGAN, 1845–1950

Date	Million Board Feet[1]	Population[2]	Per Cent of Area in Farm Use[3]
1845		1 family	
1846	0.5		
1849		6 families	
1850			0.0
1855	3.3	300	
1860		393	
1870	16.0	2,196	
1872	35.0		
1880		8,065	
1890	100.0+	11,986	5.0
1896	200.0		
1900		15,516	20.6
1910		17,872	26.0
1920		13,991	27.4
1930		11,502	24.8
1940		13,644	28.3
1950		13,371	27.0

[1] Before 1880, Robinson and Sprague (1873); 1890 and 1896, Gibson (1944).

[2] Before 1860, Foster et al. (1939); 1860 and after, U.S. Census, Population, 1870–1950.

[3] 1850 data, Robinson and Sprague (1873); Land Area in 1890, Gibson (1944); other data from U.S. Census, Agriculture, 1910–1954.

General Land Office Survey begun in 1840, although the first settler did not arrive until 1845. By 1855, the population had reached 300, and logging of the virgin timber was under way. This year marked the completion of the General Land Office Survey of the subdivision of the townships around Douglas and Burt lakes. Kilburn (1957) describes the vegetation of this time and notes that it was essentially undisturbed by Indians, fire, or settlement. Major changes in the original forest took place after this time.

By 1896, lumbering reached its peak in the county and declined thereafter. The major softwood logging was over around the turn of the century, and lumbering operations concentrated on hardwoods for the next decade. In 1955 three early settlers in the county were

interviewed about the early logging and fire history of the region. Their accounts coincided remarkably. The three were David Wolf, 82, of Riggsville, who moved to the county in 1882; Jack Spray, 75, of Riggsville, born in the county; and Noel Linebaugh, 82, of Pellston. These men reported that by 1880 all the better pine had been logged in both the Douglas Lake and Pellston areas. According to Mr. Spray, the last of this logging involved the UMBS land and occurred in the winter of 1879–80. He reported that the winter was snowless. To transport the logs, tracks had to be made out of logs, a car built, and the logs carted downhill in railroad fashion to Reese's Bog and Burt Lake and thence by water to Cheboygan. Most of the trees logged were white pine.

Hemlock logging was in progress during the 1870's, and at this time a tannin extraction factory was in operation on Burt Lake, according to Mr. Wolf. In logging, the trees were cut and the bark "ringed" around the trunk at four-foot intervals, then split down the sides and peeled. The wood was then cut up for rough lumber. The usefulness of hemlock, plus its susceptibility to fire, helped convert it from the most abundant tree in 1855 (Kilburn, 1957) to an uncommon one in 1955.

From 1880–1900 small operators were salvaging poor quality trees and dead pine snags on cutover areas, according to Mr. Linebaugh. By 1900 the conifers were gone, and attention was directed to the high-grade hardwoods. In 1902 Tindle & Jackson built a big mill in Pellston and began to cut hardwoods west of Pellston. Early hardwood lumbering concentrated on large sugar maples for veneer logs but gradually turned to other species and smaller trees as the availability of more desirable timber diminished. By 1920 hardwood logging on a large scale had ceased. Location of some of these later operations is described by botanists (Gleason, 1918; Gleason and McFarland, 1914).

The interval between 1880 and 1920 was described by both Mr. Wolf and Mr. Spray as one of constant fires. No timber remained in the pine lands, and no attempt was made to guard against fires or even to put them out. In fact, the natives regarded the fires as favorable, since they stimulated growth of blueberries and huckleberries. Mr. Spray remarked that, at times, the berries were so thick that they were removed with pronged dustpans and the leaves later removed by fanning berries and debris.

Fires kept the aspens and other timber down, so that from the hill overlooking Douglas Lake, one could see down the uncompleted railroad grade to the Douglas Lake Hotel to the west and to Germaines (west of Riggsville) to the east.

Mr. Spray claims that forest fires often started when farmers set small fires to clear the land. Mr. Wolf disagrees, claiming that farmers were usually careful of fire. He attributes most fires to carelessness by transients. Despite their disagreement on the cause of fires, the two men do agree on their frequent occurrence.

Early biologists at the Biological Station attest to the frequent forest fires both on and off the property. Voss (1956), citing Frank C. Gates in a personal communication, notes major fires in the region in 1892, 1901, 1911, and 1923. The latter date was a severe fire year and is described by Gleason (1923, p. 274), who observed that "twelve fires were counted ... in seven miles" on one summer day. Fire scars on living trees throughout the area support the statements of both the early settlers and the early biologists. These scars attest accurately both the extent and intensiveness of former fires and thus prove more valuable and reliable than the eyewitness accounts. An examination of stumps remaining from a cleared powerline strip through the Biological Station disclosed fires in the area just north of Reese's Bog and east of Carp Creek (Kilburn, 1957) in 1880, 1890, 1896, 1899, and 1907. Only a few of these trees were older than 1880, but none of those that were showed fire scars before this date. These fire scars support the eyewitness account of logging of this area in 1879–80. Furthermore, many of the smaller red pines began growth after this date. It is possible that the 1880 fire could have been a slash fire which occurred immediately after logging.

These eleven fires were recorded during a forty-four year interval, or one every four years. This high fire frequency does not mean that the entire area was burned over this often, for the data suggest numerous small fires rather than extensive ones. It merely shows the high fire frequency at the Biological Station and illustrates that reconstruction of the fire history for this area may prove extremely difficult.

Several conclusions as to the effect of settlement on the original vegetation of the Biological Station can be made. First of all, the softwood logging of pine and hemlock on the upland sandy soils of Cheboygan County took place in the interval between 1850 and 1900.

The softwood logging of the Biological Station uplands took place most certainly between 1870 and 1880. Aside from the logging of white pine in the hardwood stands and bogs, logging operations in these forest types took place at a later date. For forty years after the original logging, fires occurred at least once a decade, eliminating most of the small pines and practically all the hemlocks. In the 1920's, with the area now fire-controlled, the second-growth forests sprang up dominated by bigtooth aspen. Today, most of the older aspen stems are between thirty and fifty years of age, although, as the plant is clonal, the clones may be much older. Each forest stand may well have its own fire history, and care must be taken in transposing fire scar dates from one place to another.

It is now possible in ecological investigations at the Biological Station to proceed with some understanding of the past treatment of the vegetation; yet caution is urged, since it is apparent that any particular locale may have a very complex history.

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PHYTOSOCIOLOGICAL STUDIES OF SOME BEECH-MAPLE STANDS IN MICHIGAN'S LOWER PENINSULA

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Contrasts in the composition and reproduction of beech-maple stands in the northern and southeastern extremities of the Lower Peninsula were demonstrated by routine phytosociological surveys made in the summers of 1957 and 1958. Sixty-two phytosociological lists provide a means for testing the ideas of B. E. Quick (1924) and E. Lucy Braun (1950) about the contrasting composition of beech-maple communities from south to north by comparison of observations in these two areas.

In this paper the emphasis will be placed on the tree species only. The extent of sampling accomplished thus far is too small to permit analysis of shrub and herb strata components. The tree reproduction in the shrub and herb strata, however, provides an indication of the relative successional status of the various stands. In subsequent studies it is contemplated that shrub and herb species will be compared when additional phytosociological surveys have been completed, including those of the vernal phase as well as the aestival phase.

The authors wish to acknowledge assistance from members of the University of Michigan Biological Station ecology class of 1957, whose phytosociological lists were used for an analysis of the northern stands. The 1958 study of stands in the southeastern area is part of the senior author's current phytosociological survey of southeastern Michigan supported by National Science Foundation Grant G-5578.

The taxonomic nomenclature is that of *Gray's Manual of Botany*, 8th ed. (Fernald, 1950).

Localities and Methods

The localities and extent of sampling of the eight stands is shown in Table I. Stand numbers in this table correspond with the num-

TABLE I

BEECH-MAPLE STANDS SURVEYED

Stand No.	Name of Locality	County	Township	Town, Range, and Section	No. of Plots	Plot Size
1	Bois Blanc Island	Mackinac	Bois Blanc	Sec. 9	6	10 × 10 m.
2	Island View	Emmet	Redmon	T.37N, R.6W. Sec. 18	14	10 × 10 m.
3	Colonial Point	Cheboygan	Burt	T.36N, R.3W. Sec. 21	14	20 × 20 m.
4	Haven Hill	Oakland	White Lake	T.3N, R.8E. Sec. 19	8	20 × 20 m.
5	Proud Lake	Oakland	Commerce	T.2N, R.8E. Sec. 17	4	20 × 20 m.
6	Irwin's Woods	Washtenaw	Sharon	T.3S, R.3E. Sec. 4	4	20 × 20 m.
7	Brookville Road	Washtenaw	Salem	T.1S, R.7E. Sec. 28	6	20 × 20 m.
8	Beck's Woods	Wayne	Northville-Plymouth	T.1S, R.8E. Sec. 33	8	10 × 10 m.

bers on the map in Figure 1. Observations were recorded in the form of complete species lists, with cover-abundance and sociability estimates according to the Braun-Blanquet method (Braun-Blanquet, 1932). The scale of cover-abundance ratings used for the surveys is given in Table II.

Phytosociological lists of the plots surveyed were combined into tables for each stand. Space limitations prevent presentation here of the complete tables, which will be published elsewhere. Frequency class for each species in each stand was computed according to the following scale:

Frequency Class	Frequency Percentage
1	Less than 20%
2	20–40%
3	40–60%
4	60–80%
5	80–100%

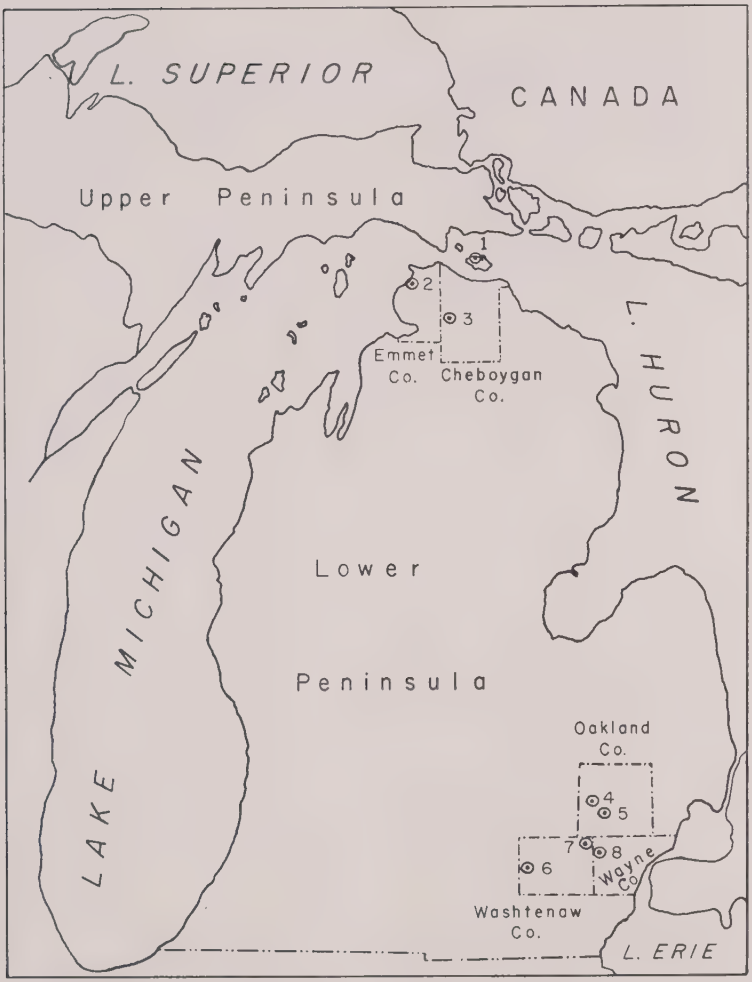

FIG. 1. Index map of beech-maple stands surveyed in the Lower Peninsula of Michigan. 1. Bois Blanc Island; 2. Island View; 3. Colonial Point; 4. Haven Hill; 5. Proud Lake; 6. Irwin's Woods; 7. Brookville Road; 8. Beck's Woods.

TABLE II

SCALE OF COVER ABUNDANCE WITH CONVERSION VALUES FOR CALCULATING IMPORTANCE (MODIFIED FROM BRAUN-BLANQUET, 1932)

Cover-Abundance Rating	Interpretation of Cover-Abundance Ratings	Conversion Value for Importance
5	Covers 75–100% of the plot, irrespective of number of individuals.	80
4	Covers 50–75% of the plot, irrespective of number of individuals.	60
3	Covers 25–50% of the plot, irrespective of number of individuals.	40
2	Numerous individuals, but covers only 5–25% of the plot.	20
1	Plentiful, but covers less than 5% of the plot.	5
+	Sparse, cover very small.	0.1
r	Rare individuals, cover insignificant.	0

Histograms of the frequency classes of tree species are presented in Figure 2.

Figure 3 presents histograms of importance values for tree species based on cover-abundance data. For calculation of importance values, a numerical value was assigned to each cover-abundance rating (*cf.* Carles, 1948) as indicated in Table II. By substituting the importance value for the cover-abundance rating for each plot, it was possible to obtain a mean importance value for each species in each stand. Figure 3 presents the mean importance values of the predominant tree species, plotted on a scale based on geometric progression. Values less than 0.25 are indicated by a dot.

DISCUSSION

Figures 2 and 3 show strong contrasts in the composition of the northern and southeastern groups of stands. Each of the following species occurs in at least two of the three northern stands: *Pinus strobus, Abies balsamea, Tsuga canadensis,* and *Betula papyrifera.* These species do not occur in the southern stands. Conversely, *Prunus serotina, Ulmus rubra, Carpinus,* and *Carya* were not recorded for the northern area stands. *Nyssa sylvatica, Juglans ci-*

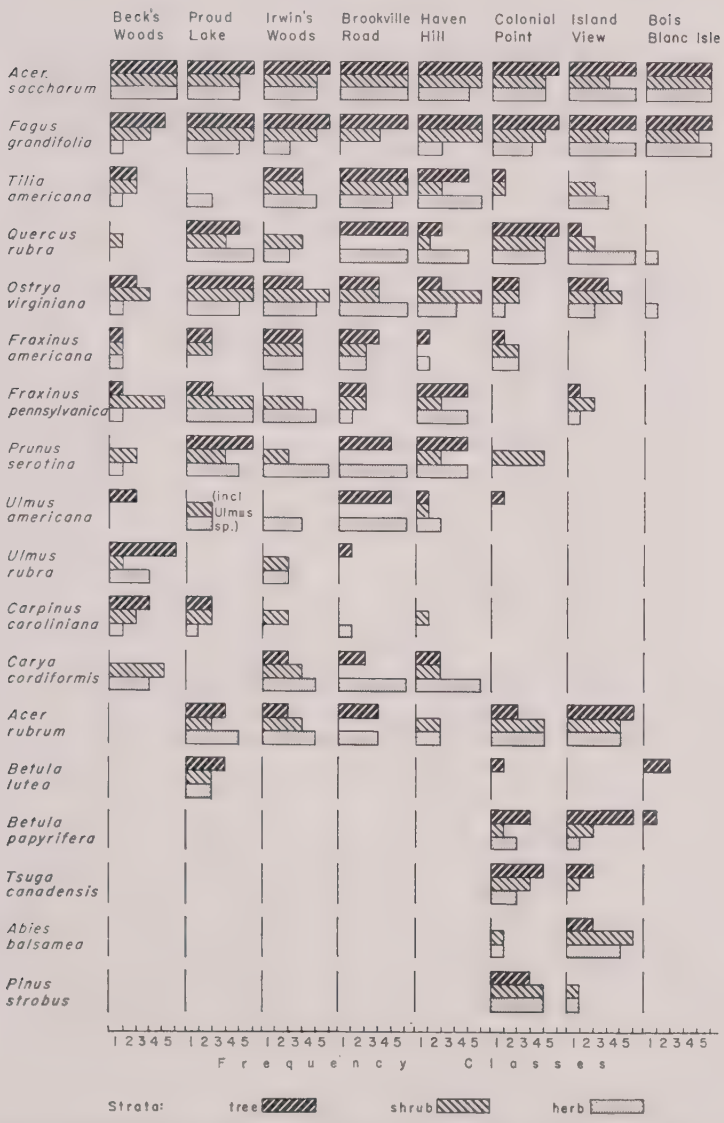

FIG. 2. Analysis of tree species in beech-maple stands by frequency classes.

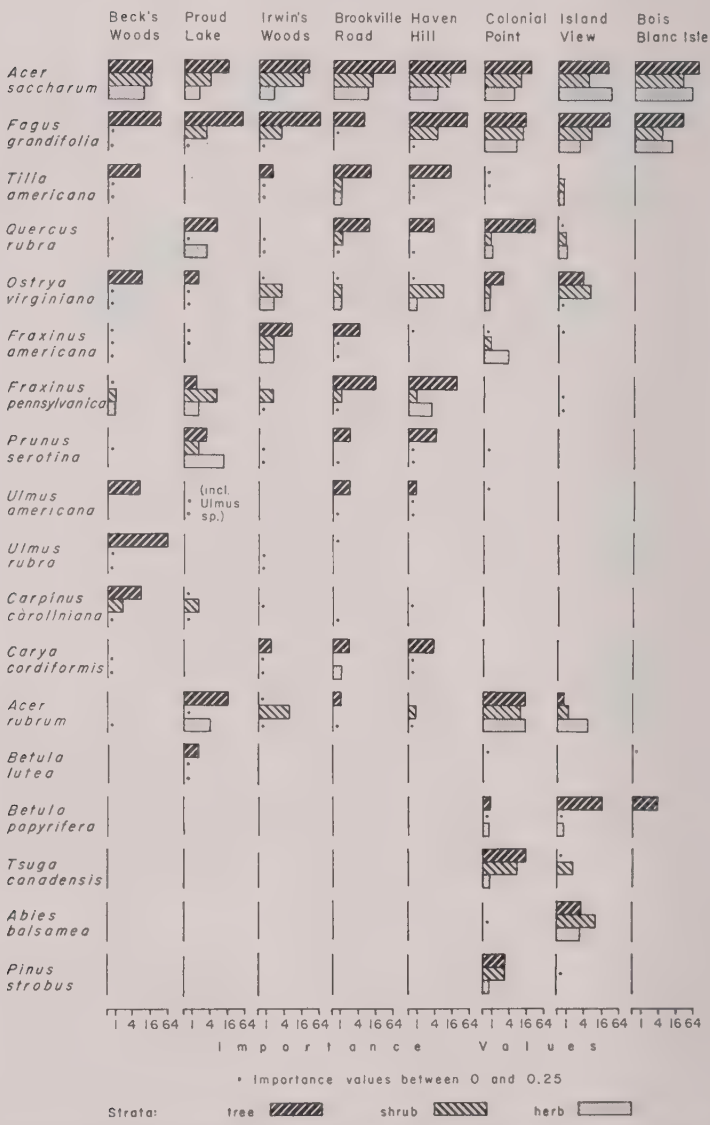

FIG. 3. Analysis of tree species in beech-maple stands by importance values based on abundance-cover estimates.

nerea, *Quercus macrocarpa*, and *Q. Muehlenbergii*, recorded by Quick (1924), did not occur in the stands observed.

Similar contrasts appear to exist in the shrub stratum of the two sets of stands, but the present sampling is inadequate for sorting out relicts from previous successional stages and transient species in this stratum. *Acer pensylvanicum* and *Vaccinium angustifolium*, for example, occurred in many of the northern plots but were not observed in the southern localities.

The differences in species composition and frequency values in the southern stands reflect some of the site differences in that area. Beck's Woods, which lies on the border between the Lake Plain and the Morainic Upland and is on a surface spotted with small, poorly drained depressions, shows high frequency and importance values for *Ulmus rubra*. Although the evidence is not presented here, *Lindera benzoin*, a predominant shrub in this stand, does not occur in any of the other stands.

The Proud Lake stand is situated on a ridge adjacent to a swamp forest. The soil profile exhibited a heavy accumulation of decaying humus over a thin podzol in the A horizon and a red-brown B horizon. This stand exhibits swamplike characteristics by the presence of *Betula lutea*, the relatively high frequency and importance values for *Acer rubrum*, and poor representation of *Tilia americana*.

The stands at Irwin's Woods and Haven Hill represent the more "typical" expression of beech-maple in southeastern Michigan. They exhibit relatively high frequency values for *Tilia americana* in all strata as well as for the beech and maple. *Fraxinus americana* and *F. pennsylvanica* are important species in these stands. *Acer rubrum*, although present, does not achieve high importance values.

The Brookville Road stand exhibits many features common to the stands at Irwin's Woods and Haven Hill. Observation of the frequency classes in the shrub stratum of this stand reveals that five species—*Acer rubrum*, *Prunus serotina*, *Quercus rubra*, *Ulmus americana*, and *Carya cordiformis*—are not present in the shrub stratum. As this particular feature is exhibited by a group of species, it is inferred that some disturbance (e.g., grazing) interfered with stand reproduction in its recent history.

In the northern area, the Colonial Point stand, near Burt Lake in Cheboygan County, and the Island View stand on a morainic ridge near the shore of Lake Michigan in Emmet County possess very

similar tree species composition. Both stands contain *Betula papyrifera, Tsuga canadensis, Abies balsamea,* and *Pinus strobus.* Balsam fir and white birch have higher importance values at Island View, whereas hemlock and white pine have higher importance values at Colonial Point.

The Bois Blanc Island stand is poor in species. The shrub and herb strata also lack the diversity of species characteristic of beech-maple communities. Several factors may contribute to this condition. The soil profile comprises a thin humus layer overlying a pebbly limestone till that is underlain by limestone bedrock at depths of less than ten feet. The climate is surely more severe on the island than it is on the mainland.

Although this study is based on a relatively small sample of beech-maple stands, and the sampled stands are not on sites of uniform character, the analyses of tree species components demonstrate fundamental differences in composition between beech-maple communities in the southeastern Lower Peninsula and those in the northern Lower Peninsula.

Conclusions

From the above observations we conclude that:

1. This analysis of tree species by frequency and importance values bears out the nonuniform composition of the beech-maple communities in the Lower Peninsula of Michigan, as recognized by E. Lucy Braun (1950) and Quick (1924). To determine whether the variants observed are subassociations or different associations in the European sense, or parts of two climaxes in the sense of Clements, will require more extensive surveys.

2. The contrasts in the stratal composition between the northern and southern stands indicate different successional characteristics. In the southeastern area, oaks, hickories, and white ash of the uplands and elms, red maple, and green ash of the lowlands are members of facies of the beech-maple community. In the northern area, balsam fir, white pine, hemlock, white birch, and yellow birch are characteristic of different successional histories of the stands as well as indicative of different site conditions.

3. B. E. Quick's (1924) concept of a degree of unity in the beech-maple communities for the Lower Peninsula is borne out by these observations; but it seems that the climax concept is greatly

strained, if not denied, by the strong contrasts in composition and successional origins.

4. E. Lucy Braun's (1950) division of beech-maple communities into a "beech-maple region" and the "hemlock-white pine-northern hardwoods, Great Lake Section" places the beech-maple communities of the Lower Peninsula in two separate forest regions (Clements' "associations"?). The basis for this division resides in evidence of the kind presented in this paper. However, the unifying character of the dominant roles of beech and maple in the stands examined here would argue against this treatment.

5. The core of the problem is the anomaly of uniformity of the dominance of beech and maple in these communities along with non-uniformity in accompanying tree species between northern and southeastern Lower Peninsula stands. We suggest that, within the Lower Peninsula, beech-maple communities are of the nature of edaphically selected segregates within the oak-hickory region in the south and within the hemlock-white pine-northern hardwoods in the north. Further investigations should seek to determine the extent to which edaphic factors, especially soil moisture regimen and type of humus, are correlated with occurrence of beech-maple communities.

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FORESTRY

PRELIMINARY REPORT ON THE SURVEY OF FOREST PLANTATIONS IN NORTHERN LOWER MICHIGAN

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Lake States Forest Experiment Station

In the last few years the need for a comprehensive study of forest plantations and their yields in Michigan has become increasingly apparent. The beginnings of reforestation date back more than fifty years, and many of the plantings, especially on public forests, are now twenty to thirty years old. Mill expansion has increased the demand for conifer pulpwood, and small amounts of wood from plantations are already arriving at the mills. During 1956 Christmas trees cut from plantations numbered 525,000.[1] Furthermore, the money spent for tree planting has been one of the largest investments made in forestry in the state. Many people are wondering how this investment looks.

In 1957 and early 1958 the Lake States Forest Experiment Station, Lower Michigan National Forest, Michigan Department of Conservation, and the Consumers Power Company surveyed the plantations in northern Lower Michigan and Muskegon, Ottawa, and Allegan counties. This survey was designed to yield mainly inventory information, such as area planted during the last fifty years; area now in established forest plantings by forest type, stand size, and stocking level; and present volume and growth. In addition, some miscellaneous information was collected about site, damage, and past treatment.

The project consisted of two parts, the first being to determine the acreage planted. We compiled existing planting records to determine planted area on public and industrial lands. It was not so simple to get acreage planted on private lands. We first had

[1] Lee M. James, "Resurvey of Christmas Tree Marketing in Michigan, 1957," Mich. Agr. Exp. Sta., Special Bull. No. 419, illus.

to find out how many trees were shipped to private planters from State and Clark-McNary nurseries, and how many were distributed through the Soil Conservation districts from other nurseries. Our summaries include all trees shipped to the study area through these organizations in units of 500 trees or more. Trees raised in private nurseries were not picked up unless they were sold through an SCS district. After summing the numbers of trees shipped, we converted these numbers to acres by temporarily assuming 1,000 trees planted an acre.

In the second major phase of the project, over 3,000 $\frac{1}{50}$-acre plots were measured in sample plantations, which were randomly selected from all plantings. The samples were distributed by decade to obtain a good sample in the early plantations where acreages were small. From this sample, area of established plantings was computed by forest type, stand size, and stocking level. To correct for the 1,000-trees-per-acre assumption, we measured the area planted with each traced shipment and found that 1,450 trees were shipped for every acre of forest plantings established on private lands.

Area Planted

The record summaries showed an estimated 660,600 acres planted to trees in northern Lower Michigan from 1906–56.

Areas of forest planting varied widely by counties, although some patterns were apparent. Counties with high public ownership tend to have large plantation areas. For example, Iosco, Oscoda, Wexford, Lake, Manistee, and Newaygo counties (Fig. 1), each with large acreages planted, all have large public ownership. Generally, planting on private lands declines across the survey area from southwest to northeast. The major planting effort is now concentrated in the western part of the survey area, with Wexford County presently having the highest planting rate.

Peak planting rates were reached on the public forests in the thirties (Fig. 2). On private lands the planting rate climbs each year. Since 1950 at least three-quarters of all planting has been on private lands.

Established Forest Plantings

The field sample indicated the present condition of the planted area. By applying the results of the field sample to the total area

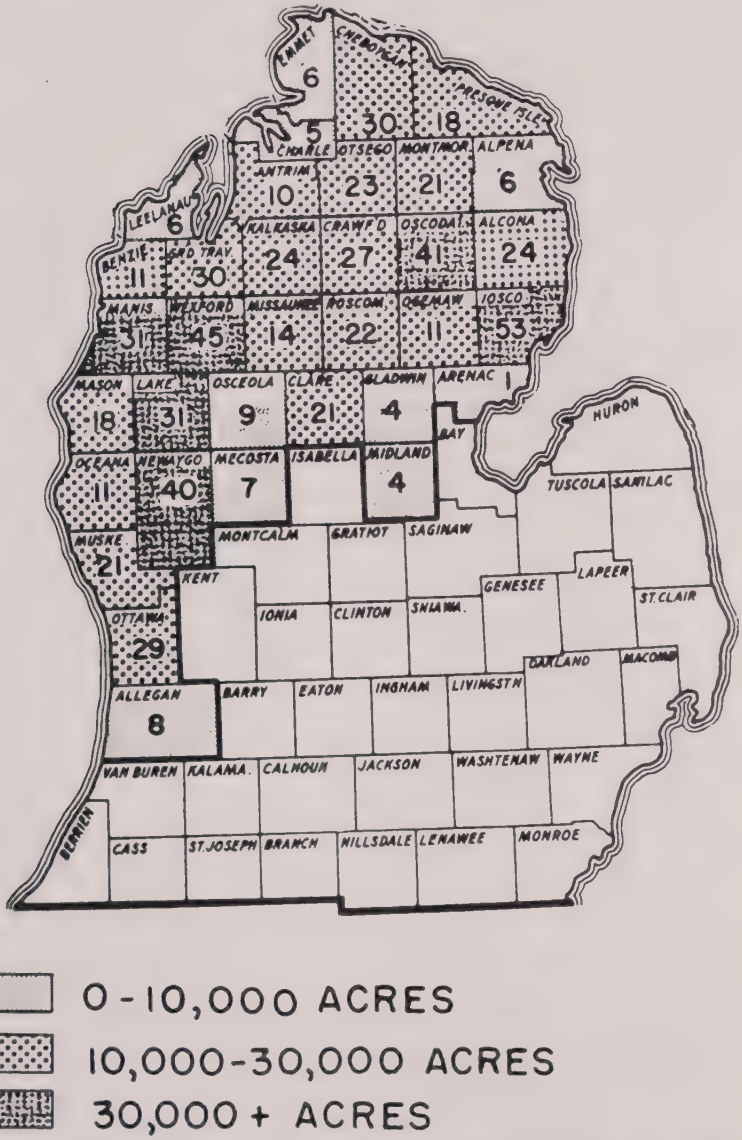

FIG. 1. Forest plantings by county, 1900–1956. The figures within each county indicate total area planted in thousands of acres.

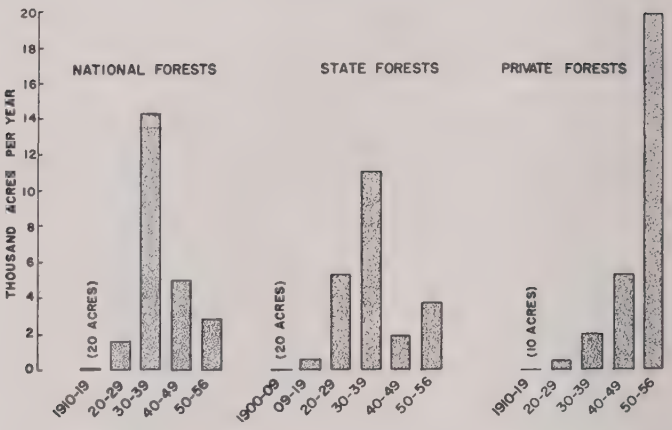

FIG. 2. Planting trends in northern Lower Michigan by owner, 1900–1956.

planted, we arrived at present acreage by forest type, stand size, and stocking level. Established forest plantings totaled 516,900 acres, or 6.6 per cent of the commercial forest land in the study block. The difference of 143,700 acres between estimated planting and the established plantations is not all due to failures; some trees were planted in windbreaks and narrow shelterbelts, while others were used to thicken up natural stands. In addition, some areas were not classed as plantations, since the planted trees were less important than the native conifers. These sweetening plantings, while only a small component of the stands they are in, should improve the stocking and ultimate yields from the area.

Only under extreme circumstances, such as burning, was a planting a complete failure. Less than 3 per cent of all planted area has reverted to grass and brush. Thirty-nine per cent of the established plantations are on the Lower Michigan National Forest, another 31 per cent are on the State forests, and 30 per cent are privately owned (Fig. 3). Distribution of established plantations by type is: red pine 53 per cent, jack pine 35 per cent, white pine 11 per cent, and spruce 1 per cent.

Fully 31 per cent of the plantations have significant native hardwood overstories, and 8 per cent have native conifer overstories (Fig. 3). Many of these plantings need release if they are to produce commercial timber in a reasonable time. Although there is a

tendency to think of plantations as solid blocks of a single species where every tree is a conifer and all are nearly the same size, few of the plantations visited were pure. The average plantation is constantly being invaded by aggressive hardwood species in addition to the trees that were there when the planting was made. It contains numerous small openings and often has a brush fringe around its border. As the plantings mature, more native trees will tend to invade the stands.

Plantations on about 62,400 acres have reached pole-timber size or larger; the rest are seedlings and saplings. However, stands on large acreages planted during the thirties are rapidly growing into pole timber; within 10 years another 74,000 acres of plantations will reach this size.

Most of the present pole timber is jack pine, totaling 40,700 acres. Other pole-timber stands include red pine with 17,400 acres, and

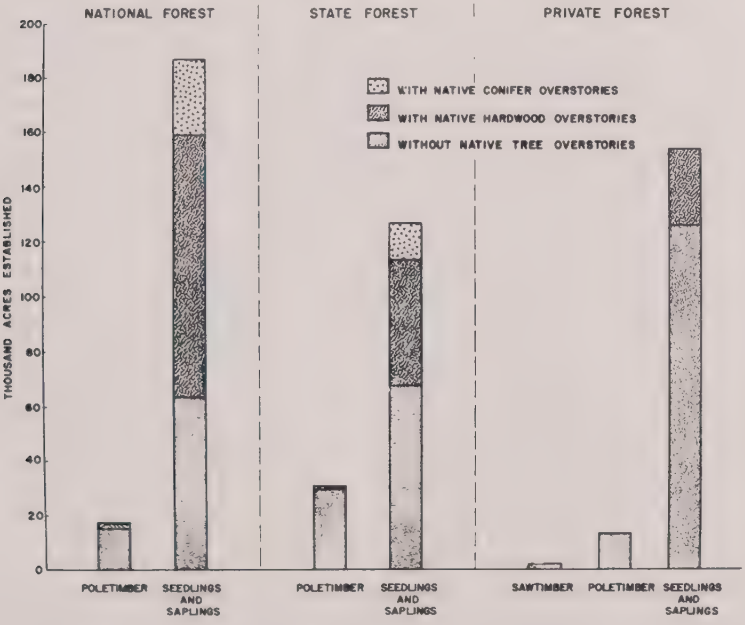

FIG. 3. Established forest plantation acreages in northern Lower Michigan by owner and size.

white pine with 3,300 acres. It is from this pole-timber acreage that the first yields will come.

Total plantation volume is increasing rapidly. Volume in planted trees over 5 inches d.b.h. is now about 585,000 cords. We obtained this estimate by determining mean volume per acre for each 10-year age class and species, then multiplying each volume by the appropriate acreage. An estimate of volume in 10 years was obtained by advancing the average age 10 years and multiplying the new mean volume by the appropriate acreage. By this method total volume in 10 years is estimated at 1,527,000 cords, and the annual growth (plus ingrowth) at 94,000 cords. The growth rate at a specific age is assumed to be the same during the near future as it was in the past 10 years.

The first yields from plantations will be as thinnings in pole-timber stands, with a minimum of about 3 cords per acre of material not needed for growth. Growth seems favorable in the younger stands where basal area is maintained in the neighborhood of 90 to 110 square feet per acre. With basal area growth of several feet per year, stands can be cut back to about 75 to 85 square feet. Present volume, in stands with 3 cords or more above this level, totals 85,000 cords. In addition, the thinnable volume on new acres reaching pole timber each year must be considered. When these are included, the volume that can be thinned from plantations during the next decade is about 15,000 cords annually.

If bolts to a 3-inch top were accepted at the mills this volume would be in the neighborhood of 15 per cent higher. One problem in profitably harvesting thinnings is that much of the volume is in "one-stick" trees where the cost of felling each tree must be charged to a single bolt. If the stands go unthinned until only 2-stick trees need be cut, growth will lag. This dilemma might be partially sidestepped if the markets would accept half sticks and sticks to 3 inches on the small end, although this would create stacking and debarking problems at some mills.

Stand Development

Little is known about the ultimate development of plantations in Michigan. Even the earlier plantings are still relatively young. For example, Beal Pinetum just east of the Michigan State Univer-

sity campus is believed to be one of the oldest white pine plantings in the State, and it is only 62 years old.

A number of factors impede the favorable development of a plantation as it progresses through the seedling and sapling stages into pole-timber size and ultimately to saw timber. Heavy ground cover of grass, low shrubs, and brush immediately slow the growth of a seedling. Browsing, insect or disease damage, and overstory competition delay it further. As a plantation closes and begins making greater demands on the soil, site quality becomes a critical factor. Development may be slowed by overstocking when needed thinnings are not made.

We found that native overstories seemed to be the most serious impediment to the transition of plantings from the seedling and sapling size to pole-timber size (Fig. 4). Where native overstories were present, growth was slower, volumes per acre were lower, and height and diameter growth was less than in plantations without

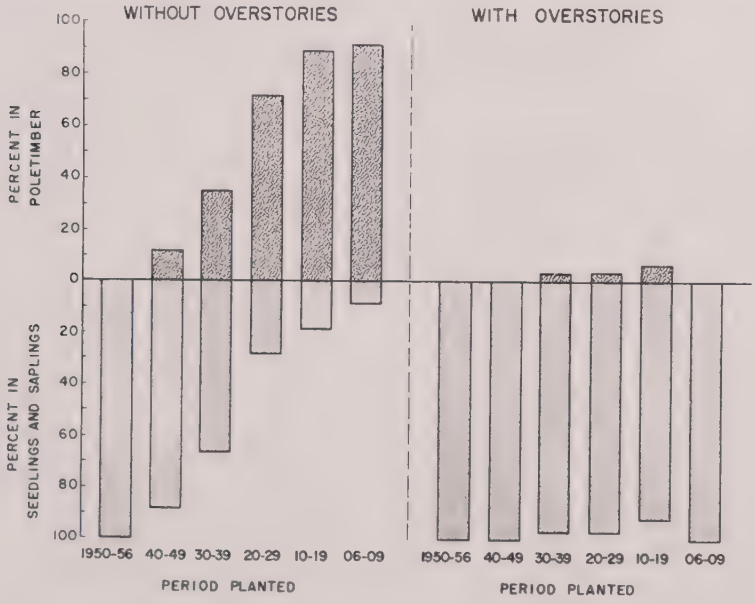

FIG. 4. Development of plantations without native overstories, and with an overstory of 3 cords or more per acre. Northern Lower Michigan, 1906–56.

native overstories (Figs. 5, 6, and 7). Over half of the plantations without overstories were of pole-timber size in 30 years, but less than 3 per cent of those with overstories of 3 cords per acre were pole timber in this time. Furthermore, planted trees under overstories

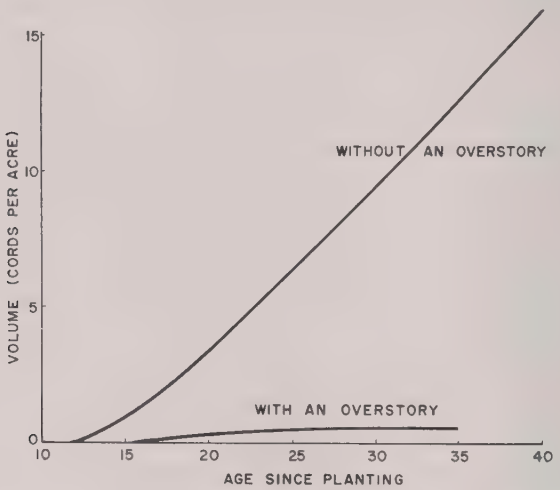

Fig. 5. Volume of red pine in plantations without a native overstory and with a native overstory of 3 cords or more per acre.

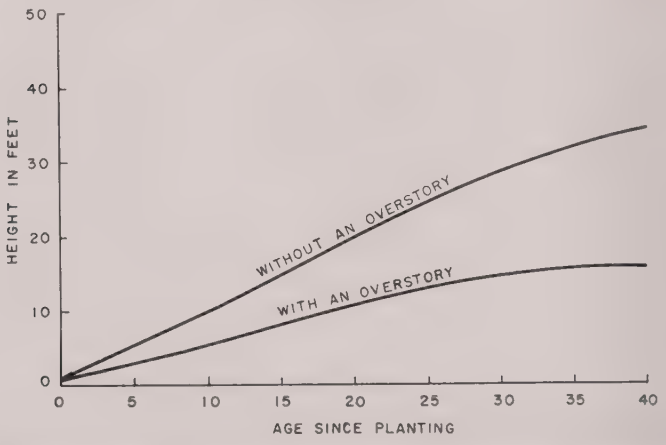

Fig. 6. Height growth of red pine in plantations without a native overstory and with a native overstory of 3 cords or more.

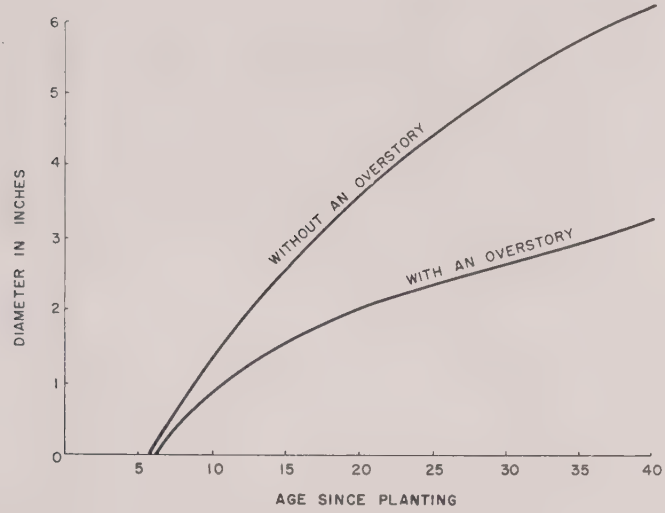

FIG. 7. Diameter growth of red pine in plantations without a native overstory and with a native overstory of 3 cords or more per acre.

are generally slim, with frail branches and thin crowns. They are easily damaged by sleet and heavy snow.

Factors other than overstories, such as insect damage, are important problems in certain localities and particular stands.

CONCLUSION

Our survey revealed that 660,600 acres had been planted in the study area during 1906–56. The planting rate on private land is rising; on public forests the rate seems stable. About 516,900 acres are in established forest plantings, with 70 per cent on public land and 30 per cent privately owned. Nearly 40 per cent of the reforested land also contains native overstories, seriously reducing the development of the planted trees. Red pine has been most widely planted, occupying 53 per cent of the established plantation acres.

Volume of trees 5 inches and larger in 1957 was about 585,000 cords. In 10 years it will be 1,527,000 cords. Growth plus ingrowth amounts to about 94,000 cords per year. Plantations of poletimber size or larger total 62,400 acres. This will more than double in 10 years. About 15,000 cords can be thinned annually from plantations during the next decade.

The results of the plantation survey of northern Lower Michigan will be published by the Lake States Forest Experiment Station in four Technical Notes and a Station Paper. Three of the Technical Notes, presenting information on acreage planted and acreage established, are available now. The last Technical Note will indicate volume and age relationships. The Station Paper, which will be a complete report of the study and its findings, is now in preparation.

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PALEONTOLOGY

A RADIOCARBON DATE FOR A WOODLAND MUSK OX IN MICHIGAN

Claude W. Hibbard and Frank J. Hinds

The University of Michigan and Western Michigan University

On October 29, 1956, Ray Coville of Climax, Michigan,[1] took three large vertebrae that he had found in a marl spreader to Frank Hinds of the Department of Biology, Western Michigan University, for identification. The marl in which the vertebrae occurred had been taken from a marl pit on the Coville farm in the southeast corner of the SE. ¼ Sec. 18, T. 3 S., R. 9 W., Kalamazoo County, Michigan.

Frank Hinds, the junior author, made two trips to the Coville marl pit prior to November 14, 1956, but failed to find additional musk-ox bones. The senior author was invited to aid in a study of the vertebrae and of the locality where they were found. On November 14, 1956, we visited the site but further work produced no other fossil bone.

The marl pit is situated in a small depression previously occupied by a lake of post-Cary age. The pit was dug in a marshy area. A small stream flowed from the pit into a nearby slough. A layer of muck, ranging from one foot to eighteen inches thick, covered the marl deposit. The depth of the marl varied from six to eight feet. Ray Coville reported that at the time of the removal of the marl which contained the vertebrae, they were operating the power shovel from four to six feet below the water surface. Due to the spring the

[1] We wish to express our gratitude to Mr. Coville for donating the musk ox vertebrae to the University of Michigan and to Carlton W. Angell for making the drawing of the woodland musk ox and the American mastodon. We wish also to express our appreciation for permission to study specimens under the care of William H. Burt and Emmet T. Hooper, of the Division of Mammals of the University of Michigan Museum of Zoology, and to William R. Farrand for making a comparison of the vertebrae with specimens in the collection at Ohio State University.

pit was full of water so that examination of the walls or floor was not possible.

The three vertebrae, No. 34124, University of Michigan Museum of Paleontology, are the atlas, axis (Pl. II, Fig. 3), and the third cervical of a large musk ox, *Symbos cavifrons* (Leidy). The vertebrae were slightly damaged by the marl spreader. It is evident that all three had been in close contact because the articular faces were clean and free from marl, and that the atlas was in contact with the skull at the time of the removal of the marl from the pit, since the proximal articular faces were clean and showed clearly the outline of the condyles of the skull. But further excavation has never revealed other bones of the skeleton.

Without doubt numerous skeletal elements of musk oxen have been encountered in excavations in Michigan. But, because of their small size when compared with the bones of the mammoth or mastodon, they have been considered merely bones of deer, elk, or domestic animals, all of which are common in muck areas. The remains of caribou went unrecognized for many years in Michigan owing to their small size.

The dorsal surface and the wings of the atlas have been broken. The anteroposterior width of the atlas from the anterior articular surface to the posterior articular surface is 77.0 mm. The atlas is more massive than the atlas of a large male *Bison bison* (No. 102162, University of Michigan Museum of Zoology). The vertebral foramen for the spinal cord is larger, and more nearly round in *Bison*, than the foramen in the atlas of *Symbos*. The atlas of *Symbos* is also larger than the atlas (No. 102448, UMMZ) of a large male *Ovibos*, the recent musk ox. The depth of the ventral wall of the atlas of *Ovibos* measured from the articular surface of the ventral arch for the dens of the axis to the tip of the ventral spine is 45.0 mm. In *Symbos* the depth is 51.0 mm.

The atlas assigned to *Symbos cavifrons* is too large and massive for *Ovibos* and *Boötherium*. It fits the skull (UMMP 3450) of *Symbos* reported by Case (1915 and 1921) from the farm of William J. Schlecht, Washtenaw County, Michigan.

The axis was the least damaged of the three vertebrae. The dorsal spinous process and the two transverse processes are missing (Pl. II, Fig. 3). The shape of the axis is shown in Plate II in comparison with the axis of *Ovibos* and *Bison*.

Measurements of Axes of Symbos, Ovibos, and Bison

	Symbos No. 34124	*Ovibos* No. 102448	*Bison* No. 102162
Greatest width across anterior face	123.5 mm.	111.5 mm.	115.0 mm.
Depth from neural canal to anterior ventral spinous process	67.0	58.5	51.0
Anterior width of neural canal	28.0	24.0	35.5
Anterior height of neural canal	25.5	21.0	30.5
Greatest width across transverse processes	99.0	82.0	74.9
Distance from midline of ventral surface of centrum to dorsal surface of a posterior articular process	130.5	105.5	107.0

The third cervical vertebra was used to obtain a radiocarbon date. The vertebra was submitted to the University of Michigan Memorial-Phoenix Project Laboratory and given No. M-639. Professor R. H. Crane gave us the date as 13,200 ± 600 B.P. in C^{14} years for the radiocarbon sample.

Very few Pleistocene mammals available for radiocarbon dates have been found in Michigan since 1950. The specimens previously collected had been treated with shellac, which made them useless for such dates. The remains of one other late Pleistocene mammal from Michigan have been dated by radiocarbon: an American mastodon (*Mammut americanus*) palate and tusk (No. UMMP 29276) recovered from beneath 2 ft. 4 in. of muck on the J. M. Bruggeman farm in Lenawee County. This adds to the evidence that some of the large mammals of Michigan became extinct only a few thousand years ago. Part of the tusk was submitted for radiocarbon dates. The outer portion of the mastodon tusk (No. M-281) gave a date of 7,820 ± 450 B.P. C^{14} years. The inner part of the tusk (No. M-280) dated 7,070 ± 240 B.P. C^{14} years. The beaver-cut limb of aspen (No. M-282) upon which the mastodon bones rested, gave a date of 9,568 ± 1000 B.P. C^{14} years (Crane, 1956; and Crane and Griffin, 1958). It may be noted that the teeth marks of the beaver on the aspen limb were the size and shape of those of *Castor canadensis* Kuhl now living in Michigan.

The above date indicates that this specimen of the woodland musk ox lived in Michigan prior to the development of the Port Huron

Moraine (Flint, 1956, p. 272). *Symbos cavifrons* was considered by Hibbard (1951) to be a woodland form, and he concluded that they foraged along the edge of the lakes and forests, with the woodland caribou in Michigan. Kitts (1953) from his study of the musk oxen arrived independently at the conclusion that *Symbos* was a woodland or steppe form.

Since Case (1915) reported the first skull of *Symbos cavifrons*

Fig. 1. Locality records of musk oxen (*Symbos* and *Boötherium*) in Michigan.

found in Michigan, parts of two other skulls have been recovered. The skull (No. UMMP 3450) reported by Case was taken about 0.5 mile northwest of Manchester, near the center of the NW. ¼, NW. ¼ of Sec. 1, T. 4 S., R. 3 E., Washtenaw County (see O. P. Hay, 1923, p. 250). The skull was found beneath four feet of muck and lay on clay. The frontal part of a skull with horn cores (No. UMMP 10566) was found in 1919 about two miles south of Hillsdale, Michigan, while a drainage ditch was being dug in a muck area. It was recovered from four feet below the surface. The posterior part of a skull with imperfect horn cores (No. UMMP 23113) was recovered from a marl pit in the farm of Max Schwanke in Antwerp Township, Van Buren County, Michigan, in 1942. For the distribution of the woodland musk oxen in Michigan, see Figure 1.

Gidley (1908) described a small and different skull type of musk ox (*Boötherium sargenti*) from the farm of Charles McKay, near Moorland, Muskegon County, Michigan. The skull was taken from two or three feet below the surface in a marsh area. It was found beneath the pelvis of an American mastodon (see Plate I). The specimen is in the Museum of Natural History at Grand Rapids, Michigan (see O. P. Hay, 1923, p. 250).

It is very likely that *Boötherium* is the female woodland musk ox since all specimens of *Symbos* based on skulls are considered as those of bulls. Kitts (1953) gives a good distributional map of all records of fossil *Ovibos*, *Symbos*, and *Boötherium* reported from North America. We do not consider *Euceratherium* reported by Kitts to be a musk ox but to belong to the tribe *Euceratherini* instead of to the tribe *Ovibovini* to which the musk oxen belong (see Hibbard, 1955, p. 80, Pls. 7–9).

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Restoration of the woodland musk ox and the American mastodon.

Fig. 1. *Ovibos moschatus*, axis, UMMZ 102448, anterior view. Reduced.
Fig. 2. *Bison bison*, axis, UMMZ 102162, anterior view. Reduced.
Fig. 3. *Symbos cavifrons*, UMMP 34124, anterior view. Reduced.

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ADDITIONAL NOTES ON THE LIZARDS OF THE CRAGIN QUARRY FAUNA

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Not long ago I published an account of some lizard fossils from the Cragin Quarry fauna of Meade County, Kansas (Etheridge, 1958). Hibbard (1955) places the fauna in the upper part of the Kingsdown formation, referred to the Sangamon interglacial of the Pleistocene. Six species of lizards, all of which are extant, were identified: *Crotaphytus collaris, Holbrookia texana, Phrynosoma modestum, P. cornutum, Eumeces obsoletus,* and *Cnemidophorus sexlineatus.* Two of these forms, *H. texana* and *P. modestum,* do not occur in the area today but range to the southwest. Two other forms, *Sceloporus undulatus* and *H. maculata,* are now common in the area but have not appeared in the Cragin Quarry fauna.

Additional lizard fossils that have become available from this locality seem to warrant some further comments on the subject. The original sample studied consisted of about 100 fossils, of which 54 could be identified. The additional material includes 140 fossils of which 71 are identifiable. All of the newly acquired fossils represent species already reported from the fauna but a number of them are elements not present in the original sample. These permit a more certain identification of one species, *Holbrookia texana,* give a clearer notion of the order of abundance of the various species, and have led to the discovery of a curious condition of sexual dimorphism in the skull of *Crotaphytus collaris.*

The fossil *Holbrookia* of the Cragin Quarry fauna was tentatively referred to *Holbrookia texana.* I was unable to find any structural differences, in the elements available, between *H. texana* and *H. maculata.* Although the latter species occurs in southwestern Kansas today and the former does not, the large size and associated lizards indicated a more probable identification of the fossils as *H. texana.* In addition to the original sample, I now have two scapulocoracoids, two maxillaries, seven frontals, one articular, one sacral vertebra, and twenty pelves. The new cranial elements permit a

more certain identification of the species. The fossil articular is like that of *H. texana* in that the retroarticular and angular processes of the element are better developed than in *H. maculata.* In addition, the new material confirms a maximum size of the fossil lizards as great as that found in modern *H. texana* and greater than that found in *H. maculata.*

A number of new cranial elements of *Phrynosoma modestum* are now available. These consist of two jugals, four squamosals, one quadrate, one parietal, three supra-angulars, one frontal, and one scapulocoracoid. Nearly all of the skull roofing bones and elements of the lower jaw are easily identified because of their ornamentation. The newly acquired elements appear to be identical with those of recent *P. modestum.*

No additional fossils of *Phrynosoma cornutum* have been recovered. The locality of the only known fossil of this species from the Cragin Quarry fauna was reported, in error, as the Cragin Quarry. The correct locality is the Cragin Quarry horizon of Mount Scott, a short distance from the Cragin Quarry itself.

Additional fossils of *Cnemidophorus sexlineatus* consist of a part of an ilium and two articulars. They differ in no way from those of recent lizards of this species.

Eumeces obsoletus is represented by an additional two maxillaries, one dentary, twelve pelves, and one caudal vertebra. The caudal vertebra is from the autonomous section of the caudal series but was recovered unfragmented, apparently because of the presence of consolidated matrix in the neural canal.

Fragments of two dentaries of *Crotaphytus collaris* are of especial interest in that they have led to the discovery of a curious type of sexual dimorphism in the lower jaw of this form. The fossil dentaries are so unusual that I originally thought the elements represented an undescribed genus of lizards. Their identity became obvious after I had compared them with skeletons of large adult males of *Crotaphytus collaris.* Eastern populations of this species exhibit considerable sexual dimorphism. The males are larger; the skull and especially the lower jaws are more robust than in the female. As in most iguanid lizards, the anterior teeth of the dentary are simple and pointed. In *Crotaphytus* this series generally contains from ten to twelve teeth, ending about at the position of the last mental foramen. In adult males, the first few teeth of the anterior simple series are

very long and slightly recurved. Following these, there is a gradual reduction in size. The posterior marginal teeth are moderately short, robust, and weakly trilobate. They become smaller toward the beginning of the series. The last few teeth of the anterior series overlap the first few teeth of the posterior series, the former being lingual to the latter. The overlap occurs about one third of the way back from the symphysis to the end of the entire tooth series. The teeth of the two series may alternate or be opposite one another. The lateral alveolar border in this region bulges out over the superior lateral face of the dentary. I know of no other lizard in which such overlap occurs. Females and subadult males of the species differ from adult males in that all of the marginal teeth are of about the same height, and there is no overlap between the simple and trilobate series.

The two fossil fragments (Fig. 1) are parts of a left and right dentary in the region of overlap. The teeth are badly worn; otherwise the positions of the mental foramina, the open Meckel's groove, and the general configuration of the elements are identical with those of recent adult male *Crotaphytus collaris.*

A total of 125 lizard elements have now been identified from the Cragin Quarry fauna. These are divided among the species as follows: *Holbrookia texana* 51, *Eumeces obsoletus* 28, *Phrynosoma modestum* 24, *Crotaphytus collaris* 20, *Cnemidophorus sexlineatus* 4, and *Phrynosoma cornutum* 1. The order of abundance based upon the minimum number of individuals which must be present in the total sample (that is, the number of the most abundant single element for each species) is as follows: *Holbrookia texana* 12 right pelves, *Eumeces obsoletus* 8 right pelves, *Crotaphytus collaris* 5 right dentaries, *Phrynosoma modestum* 4 left squamosals, *Cnemidophorus sexlineatus* 2 right dentaries, and *Phrynosoma cornutum* 1 parietal. This order of abundance is in agreement with that derived from the total number of elements of each species, except that the positions of *Phrynosoma modestum* and *Crotaphytus collaris* are reversed. These figures were not taken into account in my consideration of the paleoecological implications of the fauna, yet they are in general agreement with the conclusions drawn from other data. Of especial interest is the rarity of *Cnemidophorus sexlineatus.* The order of abundance is about what one would expect in a modern lizard fauna composed of the same species, except that *Cnemidophorus sexlineatus* would probably be one of the more common forms. I had previously

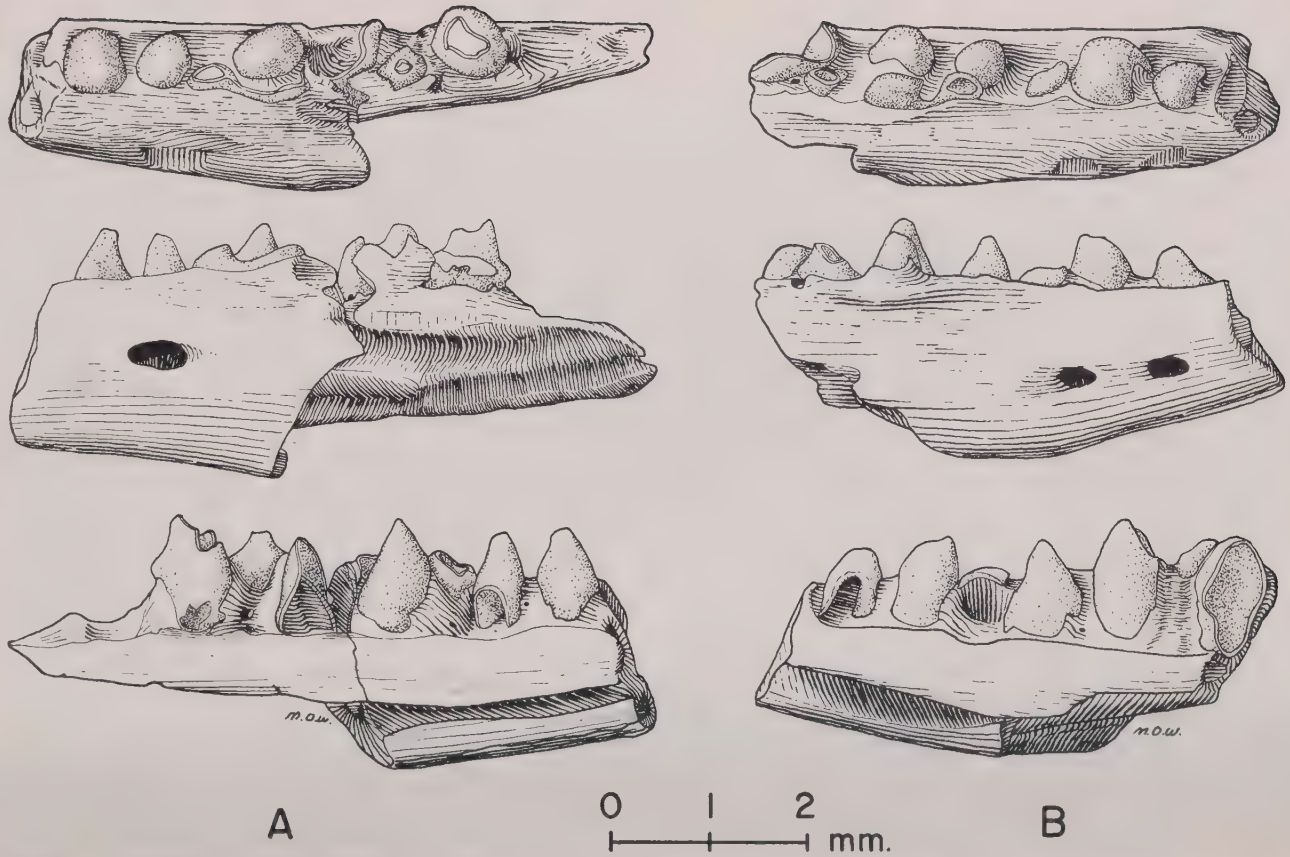

Fig. 1. A. *Crotaphytus collaris*, UMMP No. 39694, adult male, fragment of a left dentary at the region of overlap between the anterior and posterior tooth series. B. UMMP No. 33830, fragment of a right dentary from the same region.

suggested that a habitat suitable for this species was not present in the immediate vicinity of the Cragin Quarry locality during Sangamon times, a conclusion supported by the above figures for the order of abundance.

All specimens are in the University of Michigan Museum of Paleontology. The line drawings by Michael O. Woodburne were supported by the National Science Foundation (Project G-5635).

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GEOLOGY

AN EXAMINATION OF PARTS OF THE SOUTHERN COMPLEX NEAR PALMER, MARQUETTE COUNTY, MICHIGAN[1]

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The Southern Complex is composed of pre-Cambrian igneous and metamorphic rocks, predominantly granites, gneisses, schists, and basic intrusives. It embraces an area of approximately 1,400 square miles south of the Marquette synclinorium, bounded by folded Huronian rocks to the west and south and covered to the east by flat-lying Paleozoic sediments. For a century the nature and age of the Southern Complex have been subjects of controversy.

Van Hise and Leith, summarizing work to 1909, concluded that the granites were Archean and post-Huronian. Lamey (1931–1935) considered the granites mainly post-Huronian and pre-Keweenawan, and introduced the term "Republic Granite," which has since been more or less abandoned. Dickey (1936–1938) recognized Laurentian granite intruding Keewatin-type schists to form an injection gneiss; a later Laurentian granite porphyry; a post-Lower, pre-Middle Huronian granite (since proven to be pre-Huronian); and a post-Huronian, pre-Keweenawan granite, which he called Killarney. Tyler, Marsden, Grout, and Thiel (1940) recognized two pre-Huronian granites, a Huronian granite, and a post-Huronian granite. They determined these ages by the type of zircon present, the hyacinth variety indicating pre-Huronian and the malacon variety post-Huronian. Ayers (1943) considered the Republic granite porphyritic and post-Huronian.

Along the northern boundary of the Southern Complex, immediately south of the Palmer area is located the Palmer Gneiss. This narrow belt of highly metamorphosed rocks was considered by early

[1] The writers wish to express their appreciation to Dr. Justin Zinn for his help and encouragement throughout their study.

workers to be pre-Huronian. Van Hise and Leith (1911) relegated parts of the Palmer Gneiss to the Huronian period. Lamey (1935) concluded that essentially all of the Palmer Gneiss represented metamorphosed Lower and Middle Huronian.

This brief introduction perhaps illustrates the complexities with which one is faced in unraveling the problems of the Southern Complex. In reality, little detailed work has been done, considering the large area involved. The present writers have selected small areas near the northern border of the Complex (Fig. 1).

A part of Sec. 34, T. 47N., R. 26W. was mapped by Richard A. Long; Sec. 36, T. 47N., R. 26W. was mapped by Armen Sahakian; and Sec. 1, T. 46N., R. 26W. was mapped by Robert A. Vehrs.[1] It is hoped that the information thus obtained will be amplified by future work until a clearer and more detailed picture of the Southern Complex emerges.

Geology

The topography in Sec. 34 is rugged with good bedrock exposure. Only infrequent and scattered outcrops occur in the level sand plain of Sec. 1 and Sec. 36.

Granite.—The predominant rock in the area is an orange-colored albite granite. This granite frequently becomes gray at contacts. The granite is medium-grained and often exhibits a gneissoid appearance. In thin section the rock has a xenomorphic texture. The average composition is 35 per cent quartz, 25 per cent microcline and microperthite, 35 per cent albite, and 5 per cent biotite. Accessory minerals are zircon (malacon), pyrite, sphene, apatite, and rutile.

Quartz in the main part of the granite mass is relatively undeformed; but toward contacts it becomes quite strained and in places mylonitic. Frequently the quartz contains lines of highly birefringent elliptical inclusions which appear to show a preferred orientation.

Albite has an anorthite content of only about 3 per cent. It exhibits extensive alteration to paragonite in the entire area and locally to minor amounts of calcite. Combination twins of Albite, Carlsbad, and Pericline types are abundant.

Microcline is fresh and unaltered. Perthitic blades of albite often occur in the cleavage traces. In some parts of the granite a great

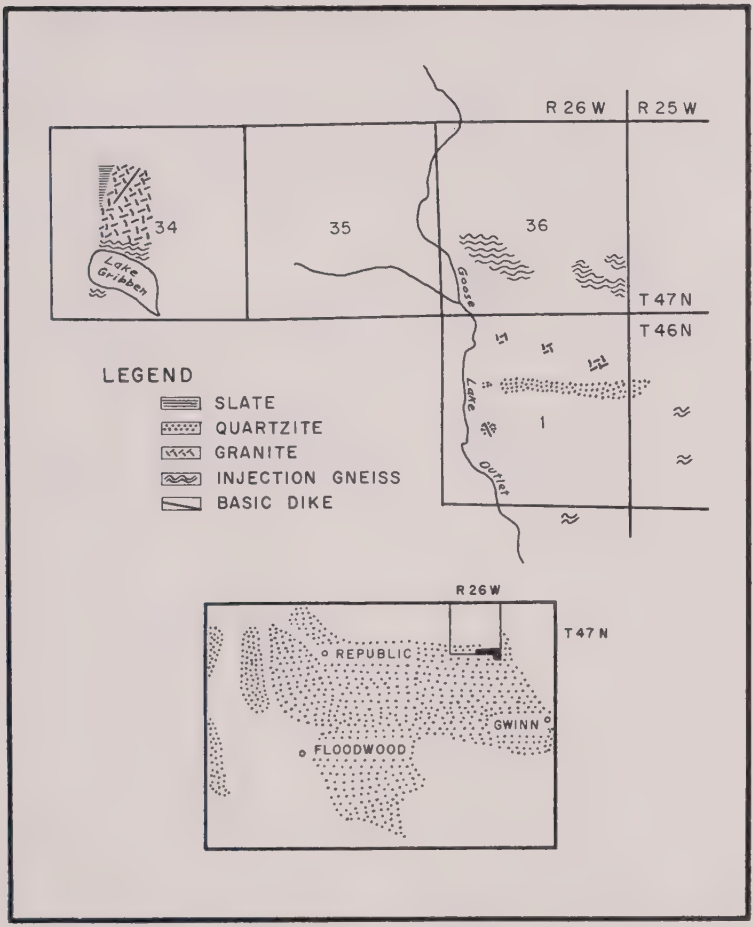

FIG. 1. Map of the area and its location in the Southern Complex of Michigan.

deal of the feldspars exhibit more complex perthites, some even showing rims of albite. Very little orthoclase was observed in any of the samples of the granite.

Biotite comprises about 5 per cent of the rock. It occurs in long, slightly oriented blades. It is always observed in some stage of al-

teration to penninite and magnetite, with elliptical masses of quartz developed along the cleavage. Locally it shows alteration to calcite and muscovite.

Zircon of the malacon type occurs in rounded to euhedral grains, almost always surrounded by a dark brown reaction rim. Rutile was observed locally as a sagenitic intergrowth in quartz. Sphene and apatite are locally abundant.

The granite is considered magmatic because of the occurrence of complex twin combinations in the plagioclase and the abundant complex perthites.

Other intrusives.—Cutting the granite are a brown-weathering, olivine diabase dike and numerous veins of aplite, pegmatite, and quartz.

Age of granite.—It is difficult to postulate an age for the granite without a more detailed knowledge of the surrounding area. We do know that the granite is cut by an olivine diabase dike which is probably Keweenawan. And that the granite is similar in some respects to Lamey's post-Huronian Republic granite.

Metamorphic Rocks

Contacts of the granite with several rock types were observed in Sec. 1 and Sec. 34. Toward the north in Sec. 34 the granite intrudes a green, quartzose slate. The slaty cleavage strikes E-W. and dips 70° N. Just north of Gribben Lake, again in Sec. 34, occur quartzose and graywacke-like rocks which exhibit a great deal of injection phenomena and are gneissose.

Quartzite.—A linear ridge of quartzite trends in an easterly direction across Sec. 1 and also outcrops in small hills slightly to the east and west. As shown in Figure 1, the granite also outcrops in several places in the northern part of Sec. 1. Stringers of this granite are found intruding the quartzite in the eastern portions. This quartzite throughout most of its exposure is a white, fine-grained, dense, homogeneous rock. Quartz is the only apparent mineral under the hand lens. Broken surfaces exhibit a sugary texture. The rock has been extremely deformed and mashed and is cut extensively by quartz veins. No evidence of sedimentary features was observed either in the field or in thin section. Red hematite staining is frequently seen.

Under the microscope the rock is seen to be composed entirely of small quartz fragments in a chlorite-sericite matrix. Cataclasis of

the quartz is prominent in all of the sections examined. Undulatory extinction and ruptural strain shadows in the quartz grains are very prevalent. Chlorite content appears to increase with increased cataclasis, reaching 20 per cent in some samples.

A quartzite outcrop west of the ridge is extremely sheared and brecciated and in places resembles a sheared conglomerate. Under the microscope this rock is seen to be large cataclastic quartz grains and fragments in a mylonitic groundmass of quartz (0.0125 mm.) and stringy bands of chlorite.

Approaching a granite contact the quartzite becomes greenish in color and scattered feldspar grains occur. Under the microscope it is seen that chlorite becomes prevalent. The quartz grains become more deformed, and small grains of albite appear. Granite intrusion and quartz veins appear to be interrelated.

A dull-green weathering dike was found cutting the quartzite. It strikes N. 45 W. and dips 70° NE. It is highly altered and is composed of chlorite, sericite, quartz, and prevalent grains of limonite.

Age and origin of quartzite.—It would be difficult at present to give an age to this quartzite or to make a definite statement regarding its origin. It resembles a quartzite described by Lamey which occurs in the Palmer Gneiss to the northwest of Sec. 1. He considers this to be Mesnard. There is no evidence, however, of a sedimentary origin for this quartzite. Jointing relationships strongly suggest at least two major deformations. This quartzite may possibly be volcanic in origin. The age problem would be simplified if the age of the intrusive granite could be determined more conclusively.

Injection gneiss.—An injection gneiss outcrops south of Gribben Lake, and in Sec. 36, and in areas adjacent to Sec. 1. It is characterized by alternating dark bands of ferromagnesians and light bands of a granitic material.

Hornblende comprises 35 to 65 per cent of the rock. The hornblende often appears in prismatic sections, mostly subhedral to occasionally euhedral. It is often accompanied by chlorite altering from biotite. Chlorite content averages 10 to 25 per cent. Some unaltered biotite is observed. There is a profusion of sphene and epidote at the contacts of the dark and light bands. Large euhedral crystals of biotite are present.

The light bands are comprised essentially of feldspar and quartz. The dominant feldspar is albite-oligoclase; it usually constitutes 50

per cent of the light bands. Orthoclase generally amounts to 15 per cent and quartz accounts for the remainder. The feldspars generally are heavily sericitized and not distinct in the dark bands; while in the light bands they appear to be relatively fresh, with original boundaries preserved, and with Albite, Carlsbad, and Pericline twinning more distinct. Quartz appears to be mylonitized at contacts. Subhedral to rounded grains of malacon zircon are present in the light bands.

The above data seem to indicate that this rock is a lit-par-lit injection gneiss. It appears that a highly liquid intrusive material invaded the cleavage or bedding planes of a rock rich in ferromagnesians. This rock is similar to the Laurentian injection gneiss described by Dickey.

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